The influence of the physical environment on invertebrate larval transport, settlement and recruitment with insights on early-stage physiological performance

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Abstract

Most marine benthic organisms have a biphasic life cycle whereby the larvae are pelagic, and their distribution, transport and settlement are largely controlled by environmental factors. Among these factors, hydrodynamics have key direct effects. Nearshore water hydrodynamics are strongly influenced by wind. This study investigated whether wind indirectly affects the distribution, settlement and recruitment of invertebrate marine larvae.

Additionally, larvae are exposed to a more constant, benign environment than they will experience after settlement, and therefore the possible effects of larval thermal history on the physiological plasticity of settled organisms was also estimated for possible long-term insights into population dynamics.

Four sites, two on the western and two on the eastern side of Algoa Bay in Gqeberha (formerly known as Port Elizabeth), South Africa, were chosen for larval collection. Sites at opposite ends of the bay were selected as they were towards either side of the dominant wind directions in this region. At each site, two sampling stations were identified at 300 and 900 metres offshore, with station replicates 300 metres apart. Sampling of marine invertebrate larvae was conducted after two days of westerly or easterly winds at either of the two western or eastern sites. The number of hours of unidirectional wind determined the prevalent wind on the two days prior to sampling. Samples were collected with a plankton pump at three depths; surface, mid-depth and bottom. Simultaneously with plankton sampling, water properties (fluorescence, temperature, zonal and meridional flow, salinity and oxygen) were measured.

Settlement/recruitment samples of mussels and barnacles were collected at six sites, two at either edge of the bay and two within the center of the bay. Plastic scouring pads and PVC

plastic plates covered with safety-walk, placed at least 30 cm from each other, were used to collect settlers/recruits of mussels and barnacles, respectively. The pads and plates were replaced on a monthly basis for 14 months to quantify monthly settlement/recruitment.

At four of the six sites used for quantifying settlement/recruitment, settlers and recruits were collected to measure the physiological responses of these two ontogenetic stages (settlers and recruits) to acute temperature variations which they might experience in the intertidal zone. Three temperature loggers were used to record real time temperature variation at each site over the period (one month) in which the artificial collectors were in position.

Factorial ANOVA was used to investigate the effects of wind, depth, site, and distance from the shore on the abundance of larvae in the water column, as well as the effects of month and site on settlement/recruitment. Additionally, multiple regression analyses were used to investigate the effects of physical parameters, including upwelling and dissipation of turbulent kinetic energy, on the abundance of both larvae, settlers and recruits. Distance-based linear models and redundancy analyses were also carried out on the abundances of invertebrate larvae. Correlation analyses were performed to investigate the effect of the number of hours of directional wind on settlement. Lastly, correlation analyses between wind and currents were carried out.

The results revealed a link between winds and currents, with wind speed directly proportional to surface current speed, which, as expected, decreased with depth. Current direction was, however, not perfectly aligned with wind direction. Larval distribution, settlement and recruitment were largely associated with the nearshore dissipation of turbulent kinetic energy and upwelling. Thus, overall larval, settler and recruit abundances were indirectly affected by wind.

Physiologically, there was no significant difference in oxygen consumption between the juvenile ontogenetic stages (settlers and recruits) of mussels. Recruits exposed to average and maximum temperatures, however, consumed more oxygen than those exposed to low temperatures. Wind and wind-mediated currents as well as temperature have been shown to shape the distribution and shore supply of larvae, and this study contributes to the broad knowledge of population dynamics and replenishment, and the tight relation of abiotic factors affecting biological processes on the shore.

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Chapter 1

General Introduction

The differences between the physical characteristics of air and water define the separation of the terrestrial and marine worlds (Agardy, 1994; Carr *et al.*, 2003; Shanks & Eckert, 2005) and related unique ecologies (Agardy, 1994; Carr *et al.*, 2003). The physiological implications of these different environments on gaseous exchange and thermal plasticity/regulation, amongst others, play a major role in shaping the differences in the ecologies of marine and terrestrial species (McQuaid, 2010; Pinsky *et al.*, 2019; Richardson & Schoeman, 2019). Terrestrial organisms are mostly vulnerable to temperature changes, as they are exposed to higher extreme temperatures than marine-based organisms, particularly in the absence of thermal refuge areas such as the shade of trees or rocks (Sunday *et al.*, 2014; Pinsky *et al.*, 2019). The thermal refuges of marine organisms, on the other hand, include deeper, cooler waters (Richardson & Schoeman, 2019), and in the intertidal zone, rock pools and crevices (Chapman, 2003; Firth *et al.*, 2013). Due to their sheltering effects, these areas are often occupied by fauna that are not found on emergent rocks or exposed areas (Firth & Crowe, 2008). Therefore, temperature can be said to have an effect on small-scale distributional patterns (Sunday *et al.*, 2012).

Variability in the environment results in differences in species distribution, abundance and composition (Richardson, 2008), thereby affecting ecosystem functions as a whole (Bernhardt *et al.*, 2020). Within the marine world, the physical stability of the system creates a distinction between the offshore and the onshore habitat, with the latter being more unstable and prone to unpredictable physical changes (McKinney, 1986). The coastline, which forms part of the onshore environment, is also characterized by high variability, instability and high unpredictability (Valentine & Jablonski, 1982; Rex & Warén, 1982) in terms of its physical parameters (Harley, 2008; Paganini *et al.*, 2014).

The world has about 1 634 701 km of coastline (Burke *et al*., 2001), stretching around 84% of the world's countries, with high ecological, economic and social importance (Martinez *et al*., 2007). These extensive coastlines include a wide variety of geomorphological features, such as soft-shores, rocky shores, flat coastal plains and cliffs (Healy, 2005; Merlin, 2005) which influence the composition of coastal communities (Visintainer *et al*., 2006; Quaas *et al*., 2019).

Within these geomorphological features, researchers in Europe and North America, dating back to the nineteenth century, have acknowledged the vertical separation of the coastline into strips or zones, with each zone characterized by its own distinctive biological features (Stephenson & Stephenson, 1949; Benson, 2002). These zone-related differences in species' occurrence are mostly a result of different environmental parameters within each zone (McQuaid, 1980; McQuaid & Branch, 1985; Branch & Branch, 2018; Bernhardt *et al*., 2020), even though some overlapping of species does occur (Branch & Branch, 2018). A huge variety of species is found in these intertidal systems, with bivalves often being a striking, dominant feature on the coastline (Strayer *et al*., 1999; Gracey *et al*., 2008).

Bivalves not only impart beauty to the shoreline, but are also of social/cultural (Vaughn, 2018; Strayer *et al*., 1999), ecological (Jones *et al*., 1994; Strayer *et al*., 1999; Vaughn, 2018) and economic (Vannarattanarat *et al*., 2013; Strayer, 2017) importance to the world. Mussels (class Bivalvia) are regarded as ecosystem engineers (Jones *et al*., 1994; Strayer *et al*., 1999), as they are capable of altering the physical structure and complexity of an environment, thereby ensuring the availability of resources for other species (Jones *et al*., 1997; Prado & Castilla, 2006). Some mussels, such as *Perna* spp. and *Mytilus* spp. compact themselves together to form strong structures (mussel beds) that affect ecosystem processes and services such as the improvement of water quality through filtration, among others (Carranza *et al*., 2009; Dame & Kenneth, 2011; Vaughn, 2018). Importantly, mussels enhance biodiversity by providing habitats for other species on local and regional scales (Jones *et al.*, 1997; Thiel & Ullrich, 2002; Prado & Castilla, 2006).

Barnacles also occur on intertidal rocky shores and can become dominant species due to their high tolerance of fluctuating conditions (Beermann *et al.*, 2013; Wrange *et al.*, 2014). These organisms are significant, as not only are barnacles used as food for humans (López *et al.*, 2005), they are also known for their ecological (Beermann *et al.*, 2013), and economic (Molares & Freire, 2003; Bedecarratz *et al.*, 2011) value in the ecosystem.

The increase in human populations along the coast has resulted in over-exploitation of intertidal communities (Branch, 1975; Hockey & Bosman, 1986; Lasiak & Dye, 1989; Agardy, 1994; Hyrenbach, *et al.*, 2000; Mannino & Thomas, 2002; Sousa *et al.*, 2018), thereby reducing the density and size of target species such as mussels (Siegfried *et al.*, 1985; Strayer *et al.*, 1999). Overexploitation leads to declines in marine biodiversity (Halpern *et al.*, 2015; Jones *et al.*, 2018), with increased spatial patchiness of populations and an ecosystem with inadvertently altered structure and function (Strayer *et al.*, 1999; Lester *et al.*, 2009).

Mussels and barnacles are used as a food source (Parmalee & Klippel, 1974; Lasiak, 1991a; Strayer *et al.*, 1999; López *et al.*, 2005) and their shells used as ornaments (Strayer *et al.*, 1999; Vannarattanarat *et al.*, 2013) by many coastal communities. Furthermore, coastal middens indicate that shellfish have been used as food by coastal communities for thousands of years (Volman, 1978; Sullivan, 1987; Lasiak, 1991a; Strayer *et al.*, 1999; Teske *et al.*, 2007; Jew *et al.*, 2013), with *Perna perna* the most commonly utilised species in the Transkei region of South Africa (Lasiak & Dye, 1989) and *Mytilus edulis planulatus* the most commonly species in New South Wales in Australia (Sullivan, 1987).

Interest in ecosystem structure and function has given rise to the investigation as to which biotic and abiotic factors affect lower-level community and population distribution patterns (e.g., Boehlert & Mundy, 1988; Bertness *et al.*, 1996; Boland, 1997; Williamson *et al.*, 2008). This type of study requires a good understanding of the relationships between the communities and their environment (Olden, 2003) as communities are structured through a combination of both biological and environmental factors at different temporal and spatial scales (Daly & Smith Jr, 1993). Biological processes such as reproduction (Fearman *et al.*, 2009) drive marine community structures (Daly & Smith Jr, 1993) through the addition of new individuals, thereby contributing to the regulation of population dynamics (Fearman *et al.*, 2009).

Many benthic invertebrates have a biphasic, bentho-pelagic life cycle, with adults in the benthic stage and larvae in the free-living pelagic stage (Thorson, 1950; 1964; Mileikovsky, 1971; Strathmann, 1974; Gaines & Roughgarden, 1985; Shanks, 1998; Pineda, 2000; Cowen & Sponaugle, 2009; Pineda *et al.*, 2010; Tiegs *et al.*, 2016; Gamoyo *et al.*, 2019; Swearer *et al.*, 2019). Larvae can live for hours, days, weeks, or even months in the water column (Shanks, 2009), and can have dispersal distances of different scales (Shanks *et al.*, 2003; Robins *et al.*, 2013) depending largely on larval development duration (Todd *et al.*, 1998; Jenkins & Hawkins, 2003; Shanks *et al.*, 2003; Einfeldt *et al.*, 2017; Bode *et al.*, 2019; Bashevkin *et al.*, 2020).

The evolution of dispersal raises the question of the order of appearance between benthic adults and the dispersing planktonic larvae in meroplanktonic species, with two main theories predominating, namely, the ‘intercalation theory’ and the ‘terminal addition theory’ (Nielsen, 2009).

The intercalation theory states that larvae developed from original holobenthic adults (Rouse, 1999; Sly *et al*., 2003; Raff, 2008; Degnan & Degnan, 2010), with arguments suggesting that dispersing larvae evolved as means to enhance rapid growth in an environment different from the adults and evade predation by colonising new habitats (Signor & Vermeij, 1994; Davidson *et al*., 1995; Peterson *et al*., 1997; Pechenik, 1999; Peterson, 2005). The terminal addition theory, however, opposes the intercalation theory, suggesting that the multicellular adult phase was a benthic addition to the primitive and original larval phase (Berrill, 1931; Jägersten, 1972; Rieger, 1994; Strathmann & Eernisse, 1994; Nielsen, 2008; 2009); with arguments that complex structures are derived from much simpler forms and therefore, multicellular organisms are modified from simple organisms (Berrill, 1931; Hedgpeth, 1974; Rieger, 1994; Arndt *et al*., 1996; Jacobs *et al*., 2005). Nevertheless, both theories acknowledge that larvae are motile and represent the dispersive phase, with benthic adults being non-motile, or at least sedentary (Reiger, 1994; Pechenik, 1999; Nielsen, 1998).

Irrespective of the order of appearance, the pelagic larval phase is the dominant dispersal stage for meroplanktonic marine species (Cowen & Sponaugle, 2009), and dispersal is key to ecological processes (Fryxell *et al*., 2008; Nathan, 2008) such as the colonization of new habitats and increased population connectivity. Differences in habitats could have led to the elimination or reduction of intraspecific competition between the larvae and conspecific adults (Roughgarden *et al*., 1994; Pechenik, 1999; Metaxas & Saunder, 2009; Robins *et al*., 2013). Spatially structured marine benthic populations are indeed mostly composed of local populations which are connected by dispersing larval stages (Revilla & Wiegand, 2008; Cowen & Sponaugle, 2009), which is the cornerstone underlying critical ecological processes (home ranging, nutrient cycling, population connectivity, competition, species coexistence) at individual, population, and community levels (Roughgarden *et al*., 1994; Pechenik, 1999;

Fryxell *et al.*, 2008; Nathan, 2008; Metaxas & Saunder, 2009; Robins *et al.*, 2013). Despite all these advantages, there are associated risks, such as larval loss or wastage due to ocean hydrodynamics (Weidberg *et al.*, 2015), as well as subsequent recruitment failure (Strayer & Malcom, 2012) that are attributed to dispersal (Nathan, 2008). Ecologically and evolutionarily, it is therefore important to understand the range of dispersal and dispersal modes of different organisms.

The ability of larvae to disperse is largely dependent on environmental factors (Zaret & Suffern, 1976; Cronin & Forward Jr, 1986; Shanks, 1986a, b; Pineda, 1994; Roughgarden *et al.*, 1994; Abelson & Denny, 1997; Dobrestov & Miron, 2001; Almeida & Queiroga, 2003; Shanks & Eckert, 2005; Marta-Almeida *et al.*, 2006; Queiroga *et al.*, 2006; 2007 Aiken *et al.*, 2007; Cowen & Sponaugle, 2009) and the organism's biological capabilities (Marta-Almeida *et al.*, 2006; Criales *et al.*, 2013) for along and cross-shore transportation. Ocean circulation is key for the exchange of material between the coastal ocean and further offshore (Pineda, 1994; Garland *et al.*, 2002; McCulloch & Shanks, 2003). Nearshore ocean circulation is affected by factors such as river outflow (Shi *et al.*, 2011; Howell *et al.*, 2012), offshore prevailing currents (Schumann, 1987; Schumann *et al.*, 1988; Goschen & Schumann; 2011), and wind (Bakun & Nelson, 1991; Brink *et al.*, 1994; Govoni & Pietrafesa, 1994; Dever, 1995; Lee *et al.*, 1999; Garland *et al.*, 2002). The effect of wind is influenced by duration and topography (Schumann & Martin, 1991), and wind plays a major role in ocean surface current direction and strength (Duhaut & Straub, 2006), which is why cross-shore water velocity is strongly correlated with alongshore wind stress (Dever, 1997).

Winds influence surface nearshore ocean current speeds and direction (Mitchum & Sturges, 1982; Shankar *et al.*, 1996; Gan & Allen, 2002). The similarity in direction between wind and surface currents has been demonstrated (Ólafsson, 1999; Kimura & Wakatsuchi, 2000). Surface wind-current synergy of directional flow is only true in equatorial regions (Boyd, 2018) and not so for non-equatorial regions (Bressan & Constantin, 2019). The balance between the frictional force (opposing wind speed and direction), Coriolis force (due to the Earth's rotation) and the wind-driven stress (due to wind speed and direction) (Bressan & Constantin, 2019) results in a deflection of the surface currents from the wind direction, to the right in the Northern Hemisphere and to the left in the Southern Hemisphere (Marshall & Plumb, 2016). The deflection angle varies from about 30° to even greater 45°, and in the water column this deflection angle increases with depth from the surface currents (Bressan & Constantin, 2019). As wind-driven currents play an important role in transporting material (Pineda, 1994; Garland *et al*., 2002; McCulloch & Shanks, 2003), frictional and Coriolis forces, together with wind stress result in these materials moving at an angle (right in the Northern Hemisphere and left in the Southern Hemisphere) away from the wind direction.

Wind-driven nearshore ocean currents play a vital role in larval dispersal (D'Aloia *et al*., 2015) and delivery to suitable habitats for attachment (Dobrestov & Miron, 2001; Queiroga *et al*., 2006). This dependence of larvae on nearshore oceanic flow (Yeung & McGowan, 1991; Graham & Sebens, 1996; McQuaid & Phillips, 2000; Kinlan *et al*., 2005; Mitarai *et al*., 2008; Pattrick & Strydom, 2008) is the cornerstone of marine community structure and overall population connectivity (Connell, 1985; Shanks & Brink, 2005; D'Aloia *et al*., 2015), as the success of benthic populations depends on successful settlement and reproduction within the parent community and/or new habitats (Pineda, 1994; Roughgarden *et al*., 1994; Abelson & Denny, 1997; Wendt & Woollacott, 1999; Pineda *et al*., 2007). Despite its importance, the spatio-temporal scales and predictability of larval dispersal and how it is regulated by wind-driven circulation are however still poorly understood (Baums *et al*., 2006; Knights *et al*., 2006; Cowen *et al.*, 2007; Pineda *et al.*, 2007), especially for marine invertebrates (Manuel *et al.*, 1996).

Biological factors such as swimming ability and behaviour also affect larval dispersal (Chia *et al.*, 1984; Metaxas, 2001; Marta-Almeida *et al.*, 2006; Criales *et al.*, 2013), as larvae can actively determine their horizontal distribution and dispersal by swimming against the weak vertical rather than the strong horizontal flow (Chia *et al.*, 1984; Metaxas, 2001). These behavioural mechanisms are taxon/species-specific (Scheltema, 1988) and depend on the developmental stage (Strathmann, 1985; Scheltema, 1988; Pringle *et al.*, 2014). Ontogenetic stage indeed plays a role in this behaviour-dependant dispersal (Cragg, 1980; Gallager *et al.*, 1996; Manuel & O'Dor, 1997; DiBacco *et al.*, 2001; Dobrestov & Miron, 2001), as swimming abilities, speeds and behaviour differ with ontogeny (Fisher *et al.*, 2000; Gravinese *et al.*, 2019).

During their development, the larvae of intertidal benthic invertebrates move from the pelagic organism to settle on a substratum between the tide marks (Pineda, 1994; Roughgarden *et al.*, 1994; Pineda *et al.*, 2007). This shift in environment from sea to land exposes the organisms to different environmental challenges (Shanks & Eckert, 2005; Tagliarolo & McQuaid, 2016). Some of these challenges include extreme thermal and oxygen fluctuations (Levin *et al.*, 2001), and therefore the physiological sensitivity of organisms to these changes might be key to their survival (Buckley *et al.*, 2001; Calosi *et al.*, 2008; Pandori & Sorte, 2019). Physiological performance of the transition stage in response to environmental stressors might be critical in predicting the distributional patterns of adults (Somero, 2002; Pörtner & Knust, 2007; Pörtner & Farrel, 2008; Horodysky *et al.*, 2015).

Environmental changes can shape species' distribution and influence geographic shifts (Peterson *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003). A better understanding of the conditions that potentially influence such shifts (including during early life stages) might be key to uncover the mechanisms that regulate population abundance and distribution (Perry *et al.*, 2005; Cheung *et al.*, 2011; D'Aloia *et al.*, 2015). Understanding the physiological performance of early life stages exposed to different environmental conditions may, therefore, be crucial to determining the tolerance of adults to possible physical stressors (Pörtner & Farrel, 2008), as sensitivity should decrease with developmental stages, as acclimatization to the new environment would have been undergone.

Respiration, measured as oxygen consumption, is a widely used estimate of metabolic rate (Davis, 1975) and that rate is used to estimate physiological tolerance to physical stressors (e.g., temperature, salinity, and pH) and to predict possible local range shifts and changes in population structure and abundances (Perry *et al.*, 2005; Cheung *et al.*, 2011). Range shifts may easily disrupt connectedness among species, and may even result in localized extinction (Peterson *et al.*, 2002; Root *et al.*, 2003) or facilitate range expansion with the invasion of new habitats (Cheung *et al.*, 2009).

In summary, the success and persistence of benthic populations depend on the effective settlement and recruitment of propagules arriving from the pelagic environment (Pineda, 1994; Roughgarden *et al.*, 1994; Abelson & Denny, 1997; Wendt & Woollacott, 1999; Pineda *et al.*, 2007), which in turn (settlement and recruitment) depend on the physiological versatility of organisms (Gibson, 1986) over and above post-settlement mortality (Bownes & McQuaid, 2009).

Aims and objectives

Port Elizabeth is a metropolitan on the south east coast of South Africa, with a population above one million and a history of heavy social inequality (Seager *et al.*, 1999). This coastal area is notoriously windy, with strong westerly winds throughout the year and increased frequency of strong easterly winds between October and November (Schumann & Martin, 1991). As in the Transkei region of South Africa (Dye *et al.*, 1997) which lies north east (about 300 km) of the study area, the coastal indigenous, low-income communities are known to use shellfish, mussels and barnacles as a source of food (Hockey & Bosman, 1986; Lasiak, 1991b; Kyle *et al.*, 1997) as it is easily accessible (Lasiak, 1991b; Nakin & McQuaid, 2014). Further east of the study site, in KwaZulu Natal, crabs are also harvested and used as a food source for humans (Kyle *et al.*, 1997). Crabs are also known to play an important role in ecosystem functioning and maintenance (Kristensen, 2008). With a growing population, there is likely to be increased intensity in harvesting eventually result in the overexploitation of these coastal resources. With increasing pressure on adult mussels, barnacles and crabs and little understanding of their dispersal and settlement mechanisms of their propagules, there is a need to examine these processes and settlement behaviour in this area.

This research therefore aimed at understanding the cross- and alongshore mechanisms of larval transport and distribution, as well as the settlement and recruitment of mussels and barnacles in relation to easterly and westerly wind regimes. With a view to better understand the influence of wind on ocean currents, the study aimed to investigate which wind-driven oceanic process is the most important driver of larval transport, distribution, and delivery. The study therefore focused on:

(1) understanding the effects of wind speed and direction on the transport and distribution of invertebrate larvae,

(2) understanding the effects of wind speed and direction on the settlement/recruitment of mussels and barnacles,

(3) coupling larval dispersal and settlement/recruitment with wind speed and direction, and,

(4) testing whether thermal history of mussel larvae plays a role in the thermal sensitivity of settlers and/or recruits.

Chapter 2

The effect of easterly and westerly winds on the transport and distribution of invertebrate larvae in the nearshore water column

2.1. Introduction

Reproductively mature benthic adults spawn or release gametes into the water column, where fertilization and larval development occurs until competency to settle on substrata is reached (Eckman, 1996; Siddik *et al*., 2018). Since larval duration varies according to taxon (Scheltema, 1972; Eckman, 1996; Shanks, 1998; Todd *et al*., 1998; Guizien *et al*., 2006; Strathmann & Strathmann, 2007; Bode *et al*., 2019), the time for larval development influences the temporal and spatial scales of dispersal (Todd *et al*., 1998; Bode *et al*., 2019), with repercussions for the structure of benthic populations (Scheltema, 1971; Roughgarden *et al*., 1984; Underwood & Denly, 1984; Gaines & Roughgarden, 1985; Levitan, 1992; Pineda, 2000; Weidberg *et al*., 2015).

In addition to the taxon-dependence of dispersal, the long-term structuring and persistence of metapopulations depends on the capacity with which larvae are retained locally or migrate over large distances (Robins *et al*., 2013; Gamoyo *et al*., 2019; Ziegler *et al*., 2020). Maintenance of local (adult) populations might therefore be a result of the local larval pools (Robins *et al*., 2013), whilst extensive dispersal (of larvae) promotes population connectivity (Cowen & Sponaugle, 2009; Selkoe *et al*., 2016).

Extensive larval dispersal can increase the range expansion of the adult populations and population connectivity through the colonisation of new, suitable habitats (Roughgarden *et al*., 1994; Pinsky *et al*., 2017; Swearer *et al*., 2019). There are, however, also disadvantages to having dispersing larvae which are not limited to, but include environmental stress, planktonic predation (Pechenik, 1999; Allen, 2008, Bashevkin & Morgan, 2020), and offshore transport (Marta-Almeida *et al*., 2006; Kumar & Feddersen, 2017), which can all result in large losses of larvae. Regardless of the advantages or disadvantages, larval dispersal largely depends on the physical water structure as well as hydrographic conditions or where eggs (mussels) or larve (barnacles and crabs) are released, as larval distribution and transport are mostly mediated by the nearshore ocean circulation (Cowen & Sponaugle, 2009; Shanks, 2009; Watson *et al*., 2010; Simpson *et al*., 2014).

Variability in nearshore circulation may result in larvae either being retained onshore or dispersed into the open sea (Marta-Almeida *et al*., 2006; Cowen & Sponaugle, 2009; Robins *et al*., 2013; Kumar & Feddersen, 2017). Along- and cross-shore water flow are among the physical features that mostly determine nearshore connectivity of benthic populations (Watson *et al*., 2010; Simpson *et al*., 2014; Bracco *et al*., 2019). Nearshore oceanic processes, such as internal tidal bores (Shanks, 1983; Pineda, 1991; 1999), surface slicks (Shanks, 1983; Kingsford & Choat, 1986), upwelling (Lutjeharms & Meeuwis, 1987; Lehmann *et al*., 2002), Stokes drift (Fuchs *et al*., 2015), and wind-generated currents (Luettich, 1999; Guizien *et al*., 2006; Weidberg *et al*., 2019) are known to play a role in the retention and/or advection of marine larvae in the water column (Marta-Almeida *et al*., 2006; Queiroga *et al*., 2006; (Fuchs *et al*., 2015).

Wind-generated upwelling, which is the process whereby currents bring deep, cold and nutrient-rich water to the ocean surface (Kämpf & Chapman, 2016), may lead to the offshore advection of invertebrate larvae if they occur at the surface of the water column (Marta-Almeida *et al*., 2006). Larval behaviour, however, can counteract this offshore advection during upwelling (Marta-Almeida *et al*., 2006; Weidberg *et al*., 2015; Weidberg *et al*., 2019). In addition, because nearshore current speeds are slow due to the drag of the shallow depth and coastline topography, larvae can be trapped in the swirling water near the shore, enhancing onshore retention (Largier, 2003).

Physical features of the nearshore water column are mostly linked to the structure of the wind (Munk, 1950; Allen, 1980; Wu, 1982; Enriquez & Friehe, 1995; Huang & Schneider, 1995;

Cerralbo *et al.*, 2016). For example, alongshore winds either result in upwelling or downwelling (the reverse of upwelling) (Lutjeharms & Meeuwis, 1987; Smith, 1988; Strub *et al.*, 1987; Lehmann *et al.*, 2002; Capet *et al.*, 2004), whilst cross-shore winds can have an effect on the structure and breaking point of waves (Feddersen & Veron, 2005). Wind can play an important role in larval dispersal through nearshore ocean circulation (Sammarco, 1994). The transport and supply of larvae to the nearshore and/or settling surfaces is mostly accomplished by onshore advection, which is caused by the wind blowing in a certain direction (Shanks *et al.*, 2000; Narváez *et al.*, 2006; Queiroga *et al.*, 2006; Queiroga *et al.*, 2007).

Along the coast of South Africa strong seasonal variation in wind structure has been documented in the main cities, with Cape Town being dominated by north-westerly and south-easterly winds, Port Elizabeth by westerly and easterly winds and Durban by north-easterly and south-westerly winds (Schumann & Martin, 1991). Regional winds drive upwelling (strong south-easterly winds in Cape Town; Nelson & Hutchings, 1983; and easterly winds around Port Elizabeth Schumann *et al.*, 1988; Goschen & Schumann, 1995), while no strong correlation between the nearshore ocean circulation and wind around Durban has been highlighted, as it experiences the weakest winds, particularly the easterly component (Schumann & Martin, 1991).

Alongshore winds are a dominant feature along the southeast coast of South Africa (Schumann & Martin, 1991), with easterly winds inducing upwelling (Goschen & Schumann, 1995). Within the context of winds affecting nearshore ocean circulation, little is known about the effects of these forces (wind speed and direction) on the distribution and transport of invertebrate larvae along the southeast coast, specifically around Port Elizabeth's Algoa Bay, South Africa. The hypothesis for this study was that persistent strong easterly winds would result in increased abundances of larvae at the western sites of Algoa Bay, while westerlies would result in increased abundances at the eastern sites of the study area.

2.2. Materials and Methods

2.2.1 Study Sites

The study took place between November 2017 and April 2018. Four sites (at least 5 km apart) were selected on the south east coast of South Africa (Figure 2.1): Cape Recife (CR) -34˚02’ S and 25˚41’ E; Algoa West (AW) -34˚01’ S and 25˚43’ E, Algoa East (AE) -33˚46’ S and 26˚17’ E, and Woody Cape (WC) -33˚46’ S and 26°19’ E. At each site, onshore (300 m from the shoreline) and offshore (900 m from the shoreline) replicated (at least 300 m apart) stations were marked using a Global Positioning System (GPS). Selection of sampling dates was done *a priori*, based on Windguru predictions, and the sampling approach was to sample after two days of either prevailing strong easterly or westerly winds, with two replicates of each wind direction on either side of the bay. Due to logistic constraints of boat availability, however, with challenging weather and sea conditions, an adapted approach needed to be taken (Table 2.1). Biological samples and physical properties of the water column were collected simultaneously at each station and replicates from on board the R/V Ukwabelana, a 13 m long, category B Lee-Cat research vessel.

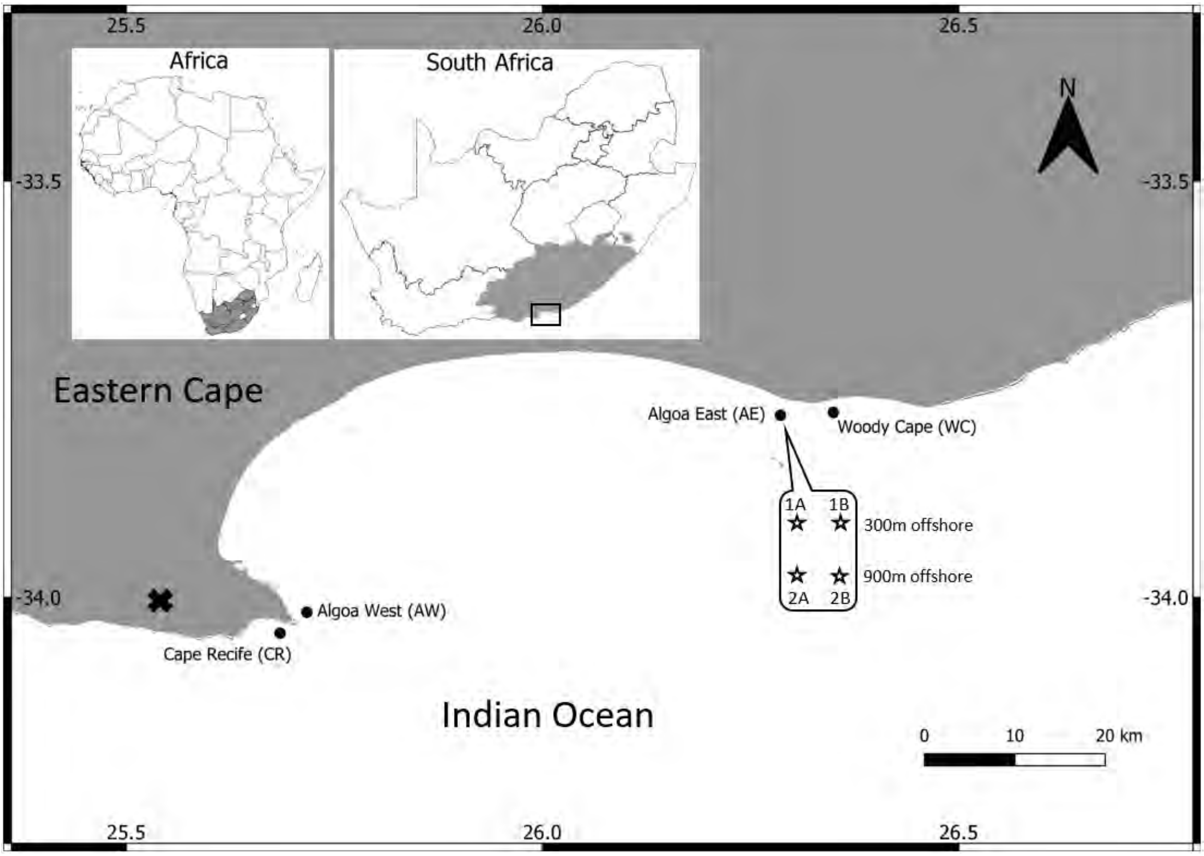

Figure 2.1: Map of the sampling sites (black circles) along the south east coast of South Africa. The stars represent the nearshore sampling design as transects (A and B; 300 m apart) at each site and the distance of the sampling stations from the shore. The black cross represents the location of the Port Elizabeth anemometer.

2.2.2 Physical data

An Acoustic Doppler Current Profiler (ADCP Workhorse Monitor Teledyne) and a CTD Seabird SBE-19 were deployed at each replicated station to obtain vertical profiles of current magnitude and direction, temperature, fluorescence, oxygen, and pH. All of the environmental data were collected at different depths which would align with biological data collection. The ADCP, screwed onto a pole attached on the outside of the vessel, faced down into the water column, and measurements were taken for at least 30 minutes or to the end of biological sampling (if biological sampling was done for more than 30 minutes; see details below). Zonal (East-West) and meridional (North-South) current flow were measured every 3–5 seconds and the data were averaged every 7–10 minutes per 1m depth, after removing values which did not pass the quality control pertaining to the percentage of good data (75%). Due to the instantaneous nature of the measurements removing tidal flows was impossible, but in any case, tidal signatures in currents were absent even when long time moored ADCPs data were analysed (Schumann *et al.*, 2005; Weidberg *et al.*, 2015).

Hourly wind speed data covering the whole sampling months were obtained from ERA5 (the fifth generation European Centre for Medium-Range Weather Forecasts - ECMWF atmospheric reanalysis of the global climate covering the period from January 1940 to present, produced the Copernicus Climate Change Service - C3S) hourly data on single levels (atmospheric, ocean-wave and land surface quantities). The pixels of the data points for wind speed were extracted according to the coordinates of the sampling sites. Hourly wind direction data were then calculated using the proxy of wind speed (zonal and meridional) on R-studio version 2002.02.3. The equation is as follows:

*Wind direction = function(u,v){(180+atan2(u,v)*180/pi)%%360}*

Where *u* is the alongshore wind speed, *v* is the cross-shore wind speed, *atan2* returns the angle in radians for the tangent *u*/*v*, and *pi* is the items response probability.

Hourly wind speed and direction data were used to calculate dissipation of turbulent kinetic energy (Wkg^{-1}) and upwelling indices (m^{3}km^{-1}s^{-1}) following Pringle (2007). Dissipation of turbulent kinetic energy was calculated using the equation in Pringle (2007):

$$\varepsilon = \frac{u^3}{kz}$$

Where u is the friction velocity at the water surface, k is the von Kármán’s constant (0.41), and z is the depth.

The wind-driven upwelling index ($m^3km^{-1}s^{-1}$) was calculated using the equation from Bakun (1973) and Weidberg *et al*. (2015):

$$UPW = \rho_a * C_D * v_{1m} * v_{1m-x} * f^{-1} * \rho_w^{-1}$$

where ρ_a represents air density (1.22 $kg.m^{-3}$, constant), C_D is the wind-drag coefficient (0.0014, constant), v_{1m} is the wind velocity at 1 metre height, v_{1m-x} is the alongshore wind component at 1 metre height, f^{-1} is the reciprocal of the Coriolis parameter (approximately $9.9*10^{-5}$ at mid-latitudes), and ρ_w^{-1} is the reciprocal of seawater density (1025 $kg.m^{-3}$).

2.2.3 Biological data

Plankton samples were collected from each station using a KC Denmark Plankton Pump Model 23.570, provided with a flowmeter and a cod end of 75 µm mesh size. The size of the mesh enabled the collection of small meroplankton such as barnacle nauplii, decapod and bivalve larvae. Plankton samples were collected from three depths, one metre below the surface of the water, hereafter referred to as ‘surface’, mid-depth (half of the total depth observed from the sea-scan on-board computer of the vessel), and 1–2 metre above the sea-floor, hereafter referred to as ‘bottom’.

The plankton pump was deployed at each depth and operated for a minimum of seven (7) minutes before being switched off and pulled back on board, after having filtered more than 1000 litres of water (calculated through the flowmeter attached to the pump). Pressurised sea water was used to rinse the pump’s mesh from the outside to wash the contents caught on the mesh into the cod end. Pre-filtered (75 µm mesh) sea water from a pressure spray was used to rinse the cod end and wash the contents into 250 ml jars filled with 99% ethanol. Samples were then transported to the South African Institute for Aquatic Biodiversity (SAIAB) laboratory at the end of each sampling event.

Meroplankton were identified (grouped according to their infraorder level) and enumerated using a Zeiss Stemi DV4 dissecting microscope. Identification of each taxon or/and ontogenetic stage was done using the guides and identification keys compiled by Sandison and Day (1954); Provenzano (1978); Booth (1983); Brown and Roughgarden (1985); Achituv (1986); Lago (1987; 1993); Shenoy and Shankolli (1993); Kadol and Kim (1996); dos Santos and González-Gordillo (2004).

2.2.4 Statistical analyses

Normality of data was tested using the Shapiro-Wilk test, while the homogeneity of variances was tested using a Bartlett test (Gokpinar & Gokpinar, 2015). To achieve homogeneity of variance, [Log_{10}(x+1)] transformation was applied, after which the data showed homogeneity of variance. Patterns of larval distribution were tested using several 4-way analyses of variance (hereafter, ANOVA) to investigate the effects of Site (4 levels, fixed: CR, AW, AE, and WC), Depth (3 levels, fixed: surface, mid-depth and bottom), Wind (2 levels, fixed: westerly and easterly), and Distance (2 levels, fixed: 300 m and 900 m from shore). For multiple tests with several taxa, a Benjamini-Hochberg False Discovery Rate (FDR) was applied to reduce the possibility of a Type I error (Benjamini and Hochberg, 1995).

Although an adaptive sampling to either prevailing easterly or westerly winds was planned and selection of dates was done *a priori* based on Windguru model predictions, the post-sampling detailed examination of wind data from ERA5 Reanalysis hourly data on single levels revealed slightly different patterns. There were three (3) south-westerly to north-westerly (hereafter westerly winds) and five (5) south-easterly to north-easterly wind (hereafter easterly winds) events sampled based on wind data for four days prior to sampling (Table 2.1). The directionality of wind was determined through the number of hours that the wind blew from a specific direction.

Table 2.1: Number of westerly and easterly hours and their respective average wind speeds for the previous four days before the sampling dates at the given sites. CR = Cape Recife, AW = Algoa West, WC = Woody Cape, and AE = Algoa East. Westerly wind events are in bold.

Dates	Sites sampled	Hours of westerly wind	Mean westerly speed	Hours of easterly wind	Mean easterly speed
25-28/11/2017	CR & AW	15	5.3	36	5.0
07-10/12/2017	WC & AE	11	8.4	53	7.5
08-11/12/2017	CR & AW	11	11.8	54	6.7
24-27/02/2018	**CR & AW**	**40**	**6.8**	**30**	**6.6**
25-28/02/2018	WC & AE	28	3.7	30	6.6
01-04/03/2018	**CR & AW**	**48**	**4.2**	**14**	**2.9**
02-05/03/2018	**WC & AE**	**54**	**3.6**	**15**	**3.3**
31/03/2018-03/04/2018	WC & AE	28	4.7	45	3.2

The potential issue of an unbalanced design was resolved through the selection of Type II rather than Type III sum of squares model (Langsrud, 2003). As multiple tests for several taxa were performed, the Benjamini-Hochberg false discovery rate (Benjamini & Hochberg, 1995) was used to reduce the possibility of a Type I error. The p-values from all ANOVAs were arranged in an ascending order, with the smallest p-value ranking as *i* = 1, the following ranked as *i* = 2, and so on. The Benjamini-Hochberg critical value was calculated using the formula:

$$B - H = \left(\frac{i}{m}\right)\mathrm{Q}$$

where i is the rank, m is the total number of tests, and Q is the false discovery rate of 0.05. The p-value that is equal to or smaller than its critical value ($B - H$ calculated value) was the cut off point for significance. Following a significant effect of any factor or interaction on larval abundances, post-hoc Fisher LSD contrast tests were performed (Ruxton & Beauchamp, 2008). These sets of biological data were analysed using Statistica 13.2.

For each sample, the taxa were added together to provide total larval abundance, and a multivariate analysis was performed to investigate the relationship between the total larval abundance and the environmental variables. A Distance-based Linear Model (DistLM) routine was used to analyse the relationship between the distribution of larval abundance and the environment variables (Raposeiro *et al*., 2011; Porri *et al*., 2014) of upwelling, dissipation of turbulent kinetic energy, zonal and meridional flow, temperature, fluorescence, oxygen, and pH. Primer 6 v6.1.15 and Permanova + v1.0.5 were used for this multivariate analysis.

Additionally, the relationship between total larval abundance and the environmental variables of upwelling, dissipation of turbulent kinetic energy, zonal and meridional flow were investigated using multiple regression analyses in Spatial Analysis in Macroecology (SAM v4.0). To avoid multicollinearity between coupled environmental variables, linearly dependant predictors were removed (Weidberg *et al*., 2015). As the time scale at which winds may have influenced larval abundances was not known *a priori*, the environmental variables were averaged over 8 different time lags (12 hours, and 1, 2, 3, 4, 5, 6 and 7 days prior to the sampling day). The Akaike Information Criterion (AIC) was used to identify the best models. A moored ADCP off the coast of Cape Recife was used for the lagging of flow data. Each time, lag data were entered separately in a multiple linear regression analysis, with total larval abundance as the response variable. For all the multivariate analyses, total larval abundance data were log transformed.

2.3 Results

2.3.1 Physical data

Wind speed and direction varied throughout the sampling days, creating increases and decreases in the turbulent dissipation of kinetic energy, and leading to periods of upwelling and downwelling (Figures 2.2–2.5). The maximum wind speed recorded for at least six sampling days was greater than 5 m/s (Figures 2.2A, C; 2.3A; 2.4A, C; and 2.5A), and of those six, easterly winds were recorded on 25-28 November 2017, 7-10 December 2017, 8-11 December 2017, 25-28 February 2018, and lastly 31 March to 03 April 2018.

Depending on the direction from which the wind was blowing, wind speeds of > 1.5 m/s induced upwelling and/or downwelling (Figures 2.2–2.5). Wind blowing at speeds > 1.5 m/s from a direction between 45° and 135° (easterly wind) induced downwelling (Figures 2.2D and 2.5B), whilst wind blowing from a direction of 225° and 315° (westerly wind) induced upwelling (Figures 2.3B and 2.4B). Depending on the wind direction, upwelling or downwelling occurs, whilst the wind speed mostly affects the turbulent dissipation of kinetic energy in the water (Figure 2.2–2.5).

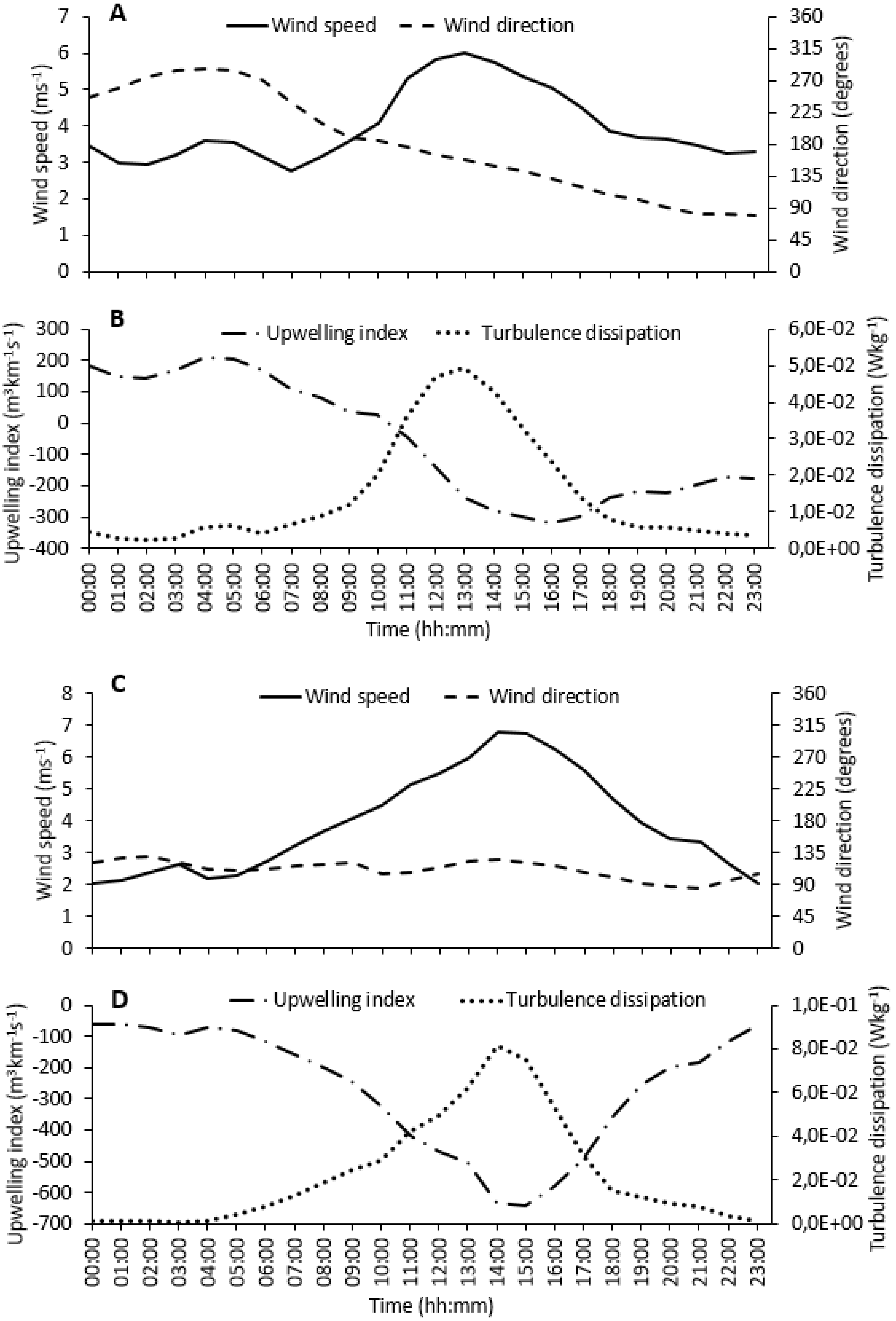

Figure 2.2: Hourly wind speed and direction (**A** and **C**) with their corresponding dissipation of turbulent kinetic energy and upwelling indices (**B** and **D**) respectively, for the sampling dates of (**A** and **B**) 29 November and (**C** and **D**) 11 December 2017.

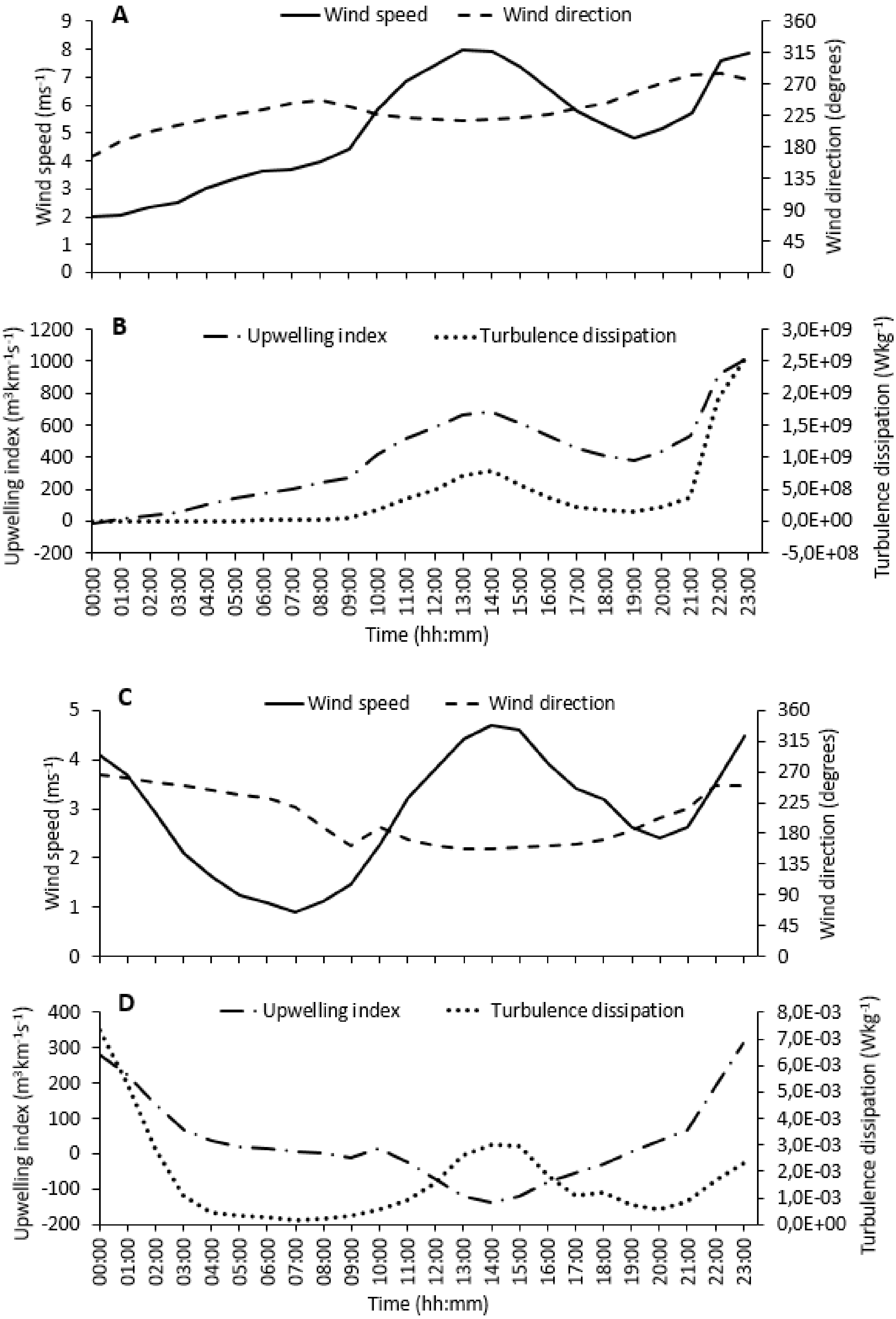

Figure 2.3: Hourly wind speed and direction (**A** and **C**) with their corresponding dissipation of turbulent kinetic energy and upwelling indices (**B** and **D**) respectively, for the sampling dates of (**A** and **B**) 12 December 2017 and (**C** and **D**) 28 February 2018.

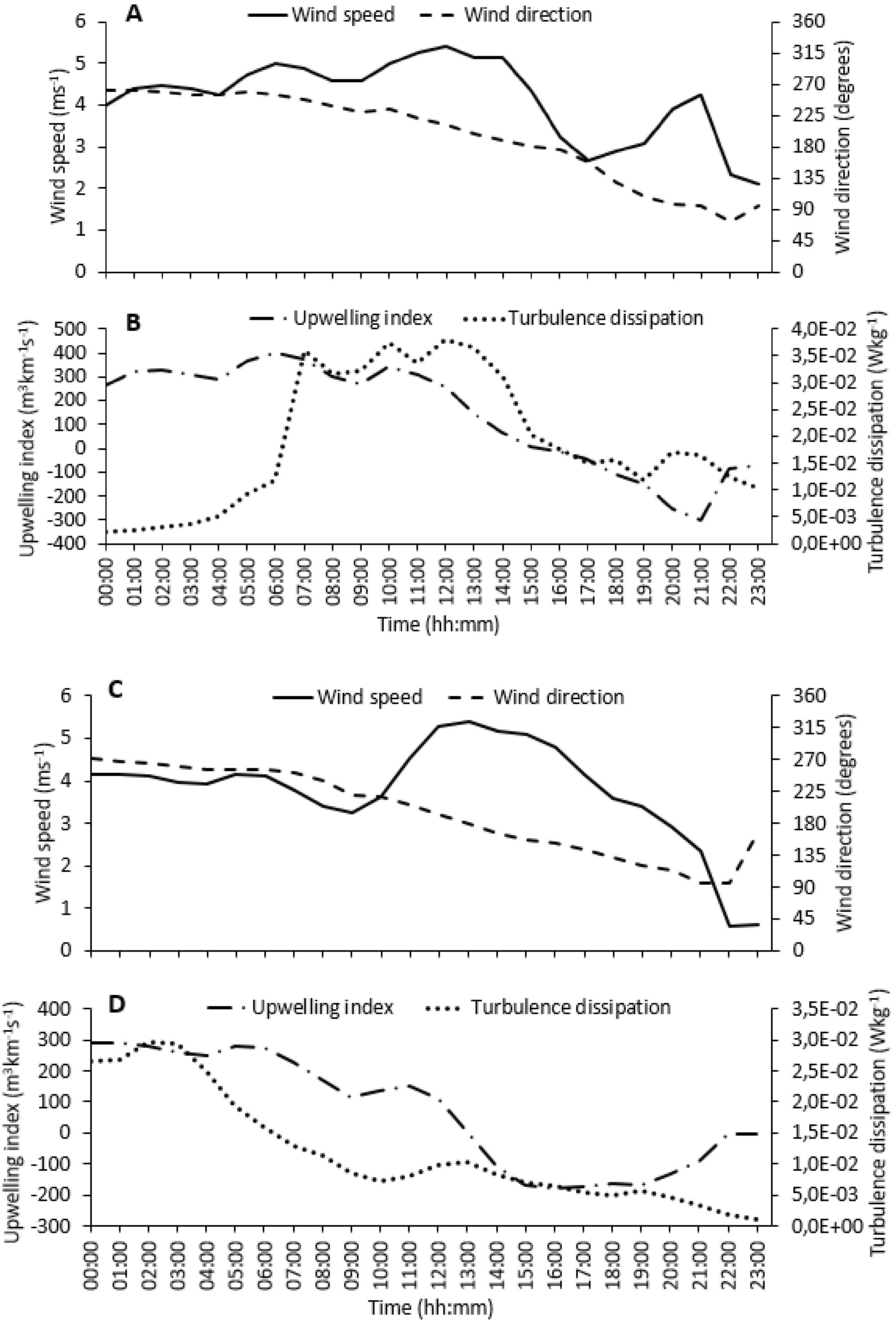

Figure 2.4: Hourly wind speed and direction (**A** and **C**) with their corresponding dissipation of turbulent kinetic energy and upwelling indices (**B** and **D**) respectively, for the sampling dates of (**A** and **B**) 1 March and (**C** and **D**) 5 March 2018.

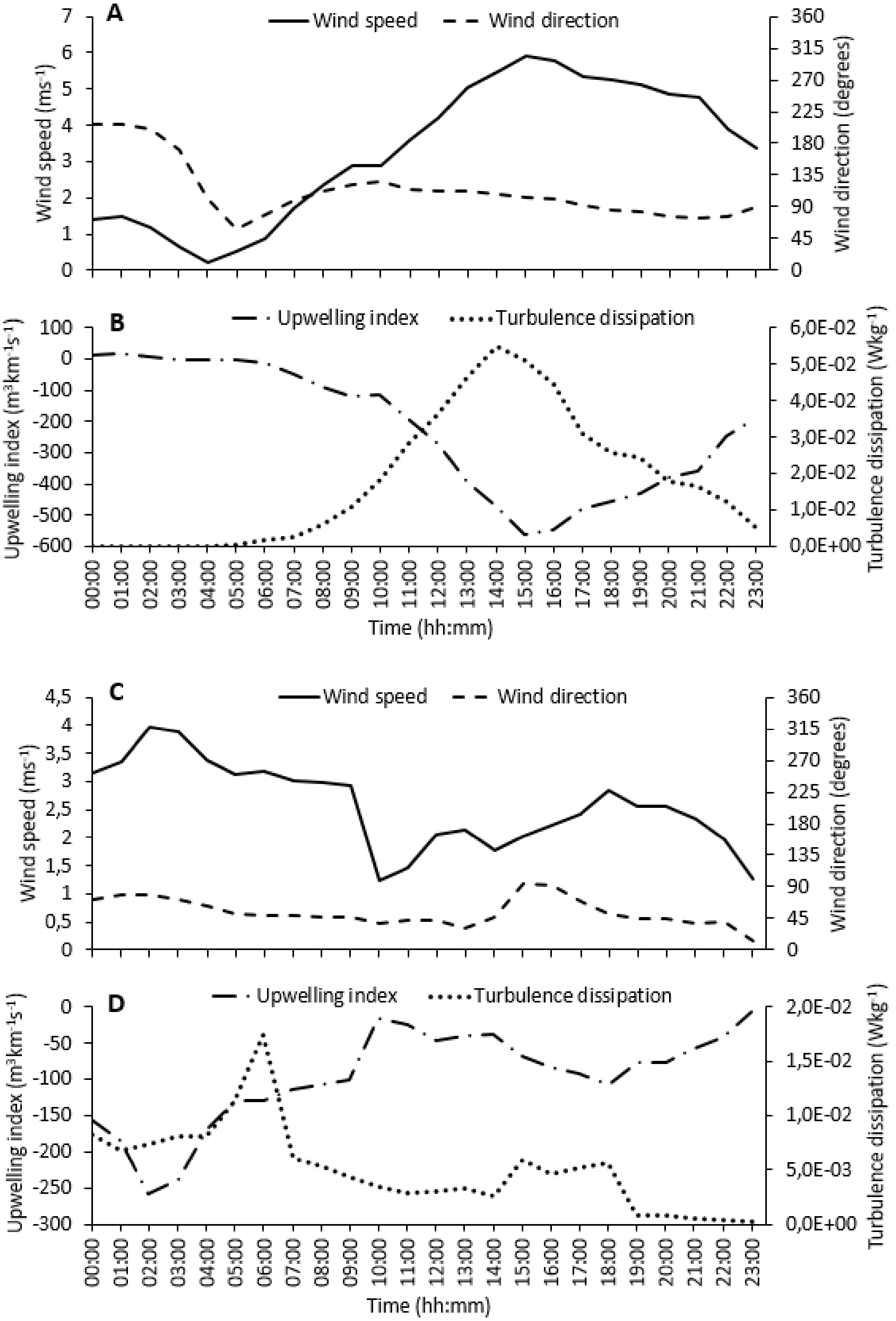

Figure 2.5: Hourly wind speed and direction (**A** and **C**) with their corresponding dissipation of turbulent kinetic energy and upwelling indices (**B** and **D**) respectively, for the sampling dates of (**A** and **B**) 6 March and (**C** and **D**) 4 April 2018.

There were significant variations in wind speed and direction seven days prior to sampling, which led to increased and/or decreased upwelling and downwelling, as well as changes in the turbulent kinetic energy in the water column (Figures 2.6–2.8). Easterly winds induced downwelling (Figure 2.6C, D on the 5th – 8th December 2017), whilst westerly winds induced upwelling (Figure 2.8A, B on the 28th – 31st March 2018). Strong winds increased the turbulent kinetic energy (Figures 2.6A, B on the 22nd and 26th November 2017; 2.6C, D on the 7th and 9th December 2017; 2.7A, B on the 22nd – 24th and 26th February 2018 and 2.7C, D on the 26th February 2018 and lastly 2.8A, B on the 28th March 2018 and 1st – 2nd April 2018). During all the sampling days, the upwelling index was always in the range of -4000 to +3000 $m^3km^{-1}s^{-1}$ (Figures 2.6D), and the turbulent kinetic energy was lowest at approximately 0.003 Wkg^{-1} (Figure 2.7B on 28 February 2018).

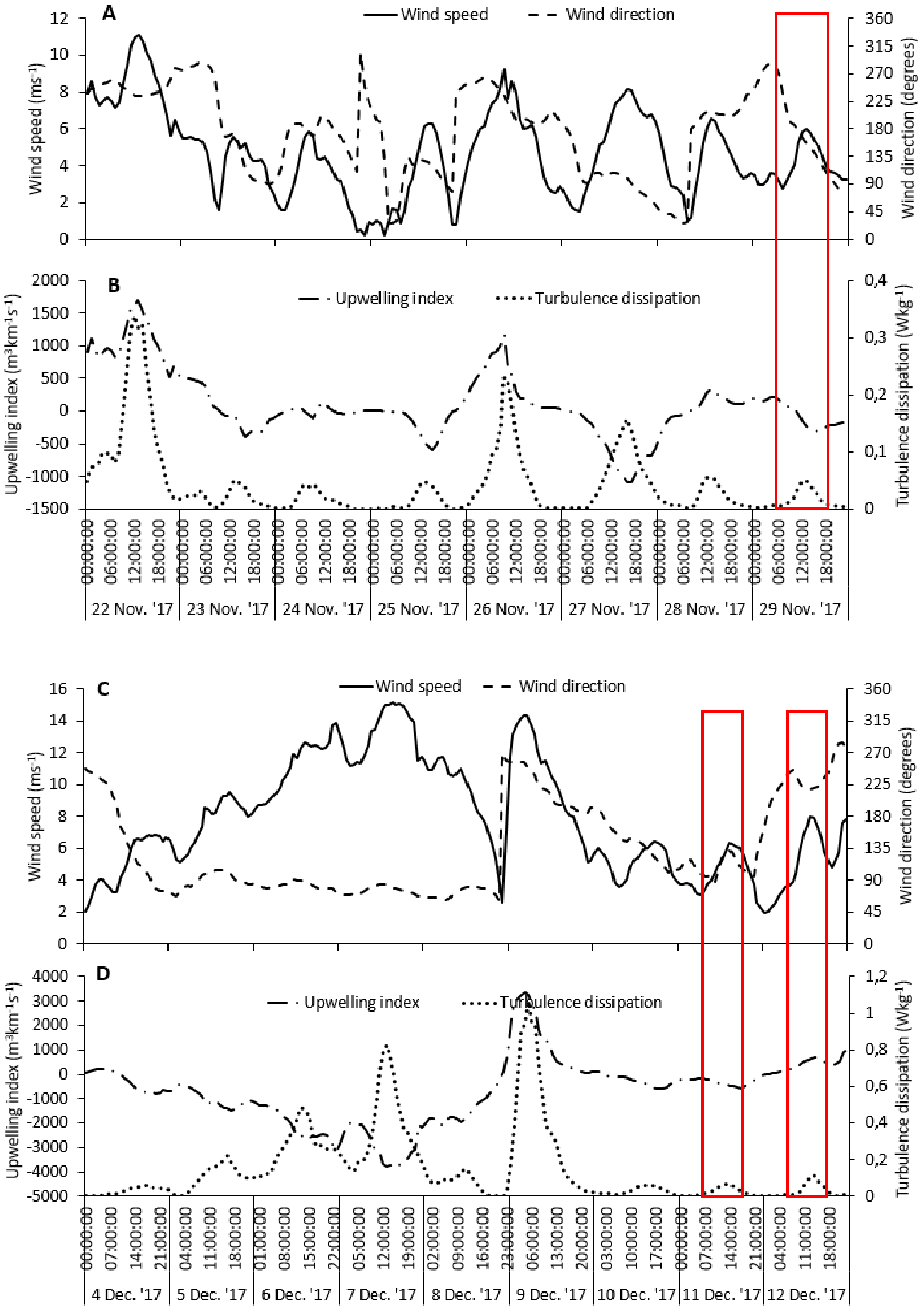

Figure 2.6: Hourly wind speed and direction (**A** and **C**) with their corresponding dissipation of turbulent kinetic energy and upwelling indices (**B** and **D**) respectively, for 7 days prior to the sampling dates of 29th November (A and B); 11th and 12th December 2017 (C and D), enclosed in red rectangles.

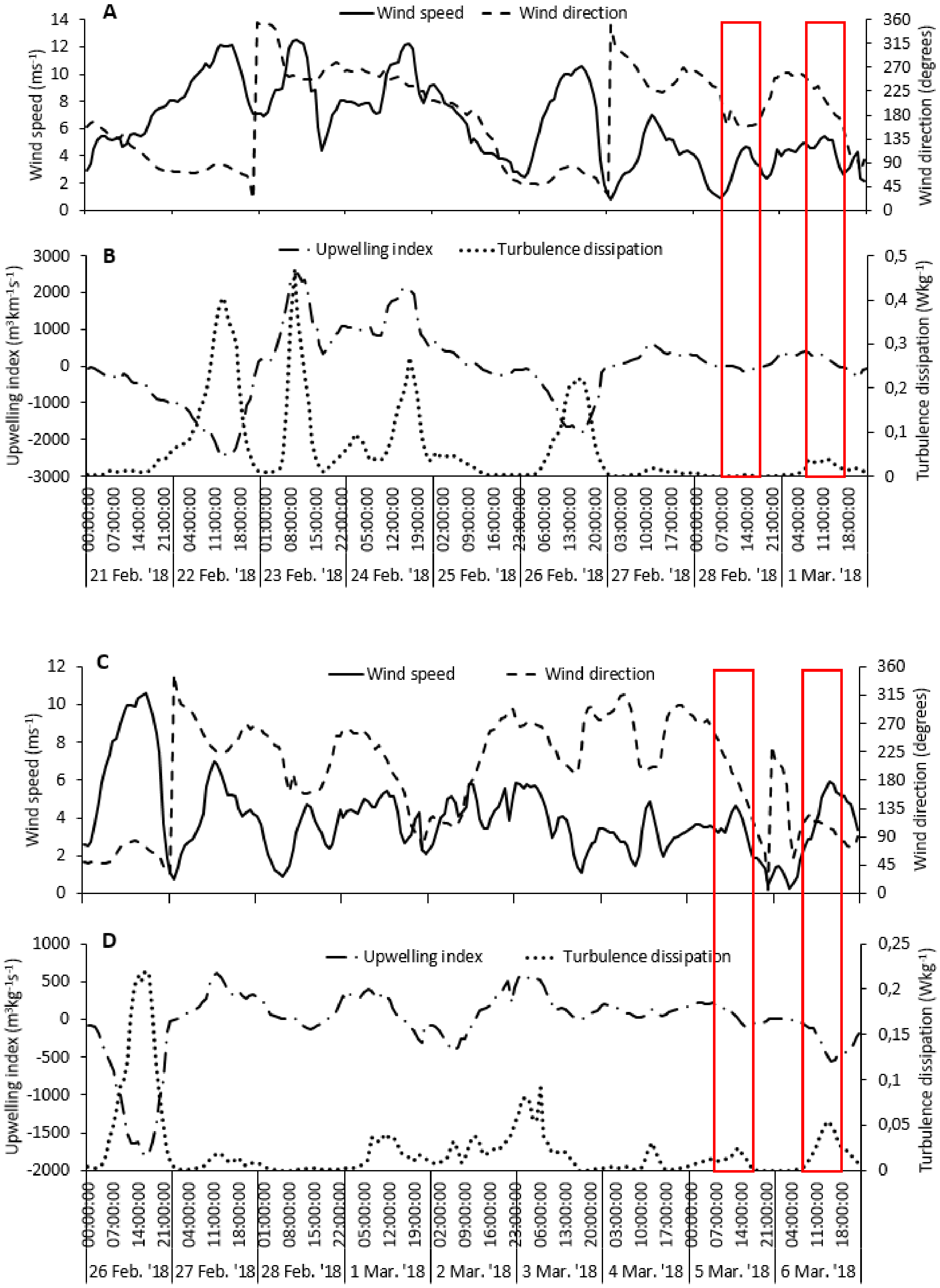

Figure 2.7: Hourly wind speed and direction (**A** and **C**) with their corresponding dissipation of turbulent kinetic energy and upwelling indices (**B** and **D**) respectively, for 7 days prior to the sampling dates of 28th February, 1st March (A and B), 5th and 6th March 2018 (C and D), enclosed in red rectangles.

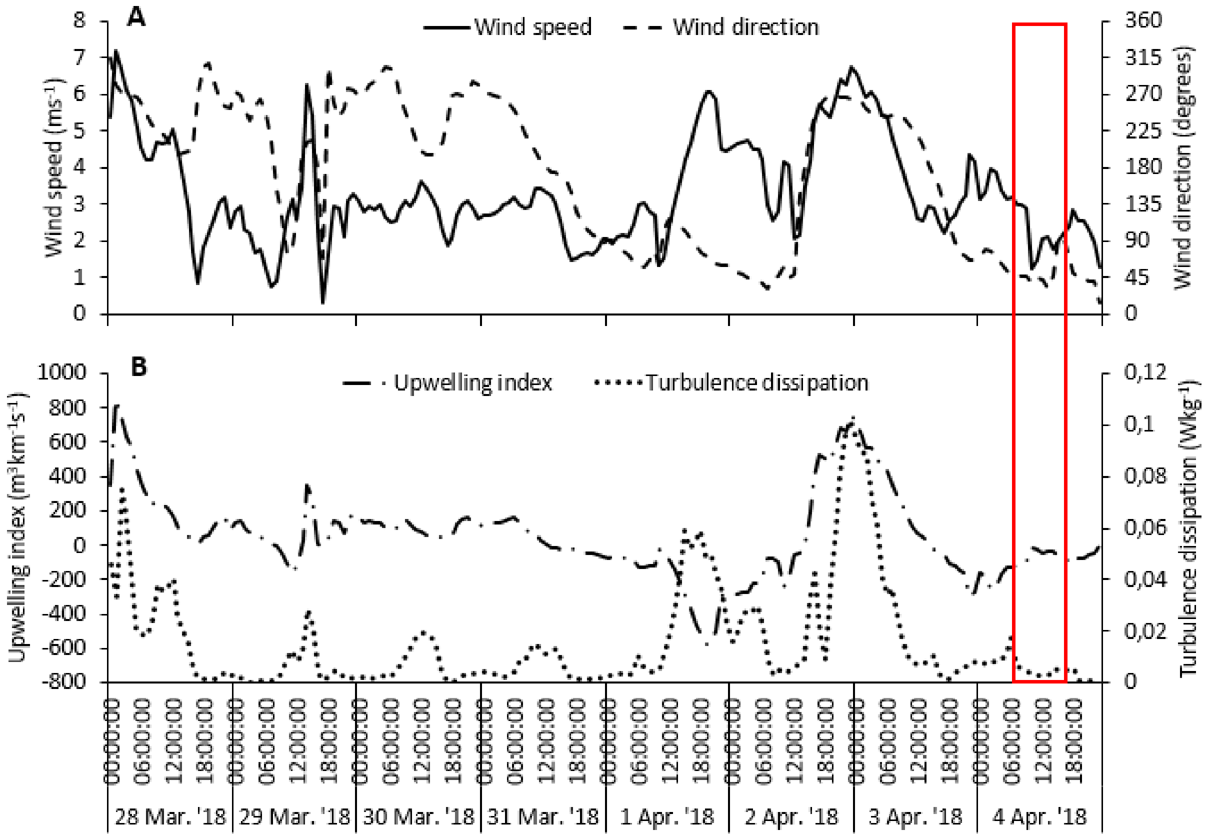

Figure 2.8: Hourly wind speed and direction (**A**) with its corresponding dissipation of turbulent kinetic energy and upwelling indices (**B**), for 7 days prior to the sampling date of 4th April 2018, enclosed in a red rectangle.

2.3.2 Biological data

Due to the multiple tests performed, the likelihood of making Type I errors was high, and to minimise this, a Benjamini-Hochberg False Discovery Rate correction was applied, which resulted in a new alpha value of 0.006 (Appendix: Table A1).

Barnacle nauplii

There was no significant effect of the all of the factors (Site, Wind, Depth and Distance) and interactions tested on the abundance of barnacle nauplii (Table 2.2).

Table 2.2: ANOVA examining the effects of Site, Wind, Depth, and Distance on the abundance [$\log_{10}(x+1)$] of barnacle nauplii. SS – Sum of Squares; df – degrees of freedom; MS – Mean Squares; F – F-ratio; and p – p-value (significant values are in bold).

Effect	SS	Df	MS	F	p
Site	3,405	3	1,135	3,152	0,027
Wind	0,413	1	0,413	1,147	0,286
Depth	3,493	2	1,746	4,850	0,009
Distance	0,077	1	0,077	0,213	0,645
Site*Wind	2,829	3	0,943	2,619	0,053
Site*Depth	0,374	6	0,062	0,173	0,984
Wind*Depth	0,266	2	0,133	0,370	0,691
Site*Distance	0,292	3	0,097	0,271	0,847
Wind*Distance	0,879	1	0,879	2,440	0,120
Depth*Distance	1,209	2	0,605	1,679	0,190
Site*Wind*Depth	1,089	6	0,182	0,504	0,804
Site*Wind*Distance	0,763	3	0,254	0,706	0,550
Site*Depth*Distance	0,710	6	0,118	0,329	0,921
Wind*Depth*Distance	0,085	2	0,042	0,118	0,889
Site*Wind*Depth*Distance	1,317	6	0,220	0,610	0,722
Error	51,848	144	0,360		

Barnacle cyprids

The results from the 4-way ANOVA performed on the abundance of barnacle cyprids revealed a significant effect of the interaction with Site and Wind (Table 2.3), which is indicative of a change in abundance at the different sites due to either wind regime. Algoa West had statistically higher abundances of cyprids than the other sites when the wind was blowing from west to east (westerly winds), with the lowest abundances at Algoa East (Figure 2.11). Depth also had an effect on the abundance of barnacle cyprids (Table 2.3), with statistically higher abundances at the bottom than the surface and mid-depth (Figure 2.12).

Table 2.3: ANOVA examining the effects of Site, Wind, Depth, and Distance on the abundance [$\log_{10}(x+1)$] of barnacle cyprids. SS – Sum of Squares; df – degrees of freedom; MS – Mean Squares; F – F-ratio; and p – p-value (significant values are in bold).

Effect	SS	Df	MS	F	p
Site	4,841	3	1,614	7,718	**<0,001**
Wind	0,325	1	0,325	1,555	0,214
Depth	6,516	2	3,258	15,581	**<0,001**
Distance	0,000	1	0,000	0,002	0,962
Site*Wind	3,695	3	1,232	5,890	**0,001**
Site*Depth	0,349	6	0,058	0,278	0,946
Wind*Depth	0,021	2	0,010	0,050	0,952
Site*Distance	0,621	3	0,207	0,989	0,400
Wind*Distance	0,226	1	0,226	1,079	0,301
Depth*Distance	0,233	2	0,116	0,556	0,575
Site*Wind*Depth	0,711	6	0,118	0,566	0,757
Site*Wind*Distance	0,289	3	0,096	0,461	0,710
Site*Depth*Distance	0,875	6	0,146	0,697	0,652
Wind*Depth*Distance	0,193	2	0,096	0,461	0,631
Site*Wind*Depth*Distance	0,144	6	0,024	0,115	0,995
Error	30,108	144	0,209		

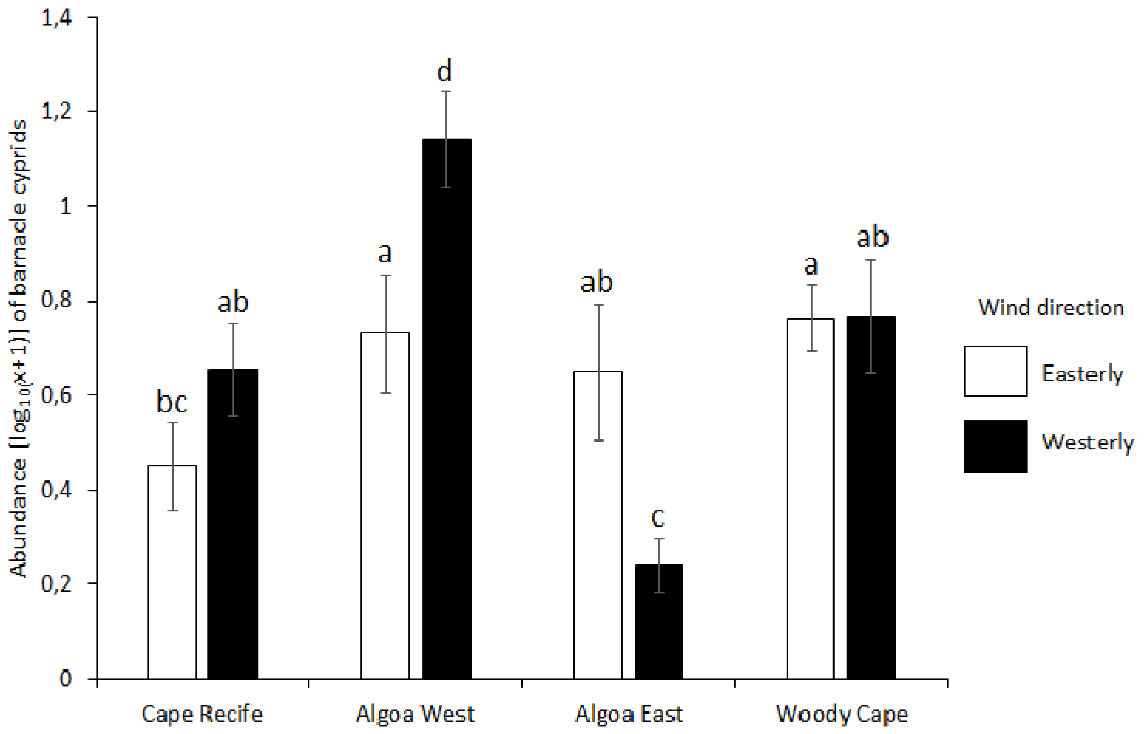

Figure 2.11: Abundance [$\log_{10}(x+1)$] of barnacle cyprids with the significant effect of Site and Wind direction. The letters above the histogram bars indicate homogenous groups across sites per wind direction identified by a pairwise test performed on the effect of the interaction of Site and Wind. Error bars indicate standard errors.

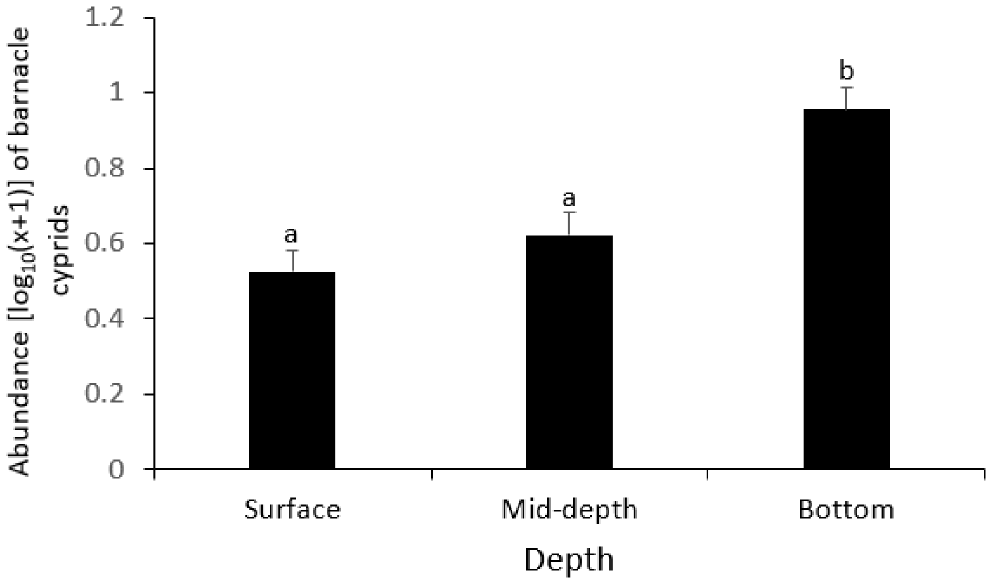

Figure 2.12: Abundance [$\log_{10}(x+1)$] of barnacle cyprids with the significant effect of Depth. The letters above the histogram bars indicate homogenous groups across depths identified by a pairwise test. Error bars indicate standard errors.

Bivalve veligers

There was a significant interaction between Site and Distance which affected the abundance of bivalve veligers (Table 2.4), pointing to a difference between sites regarding the effect of distance offshore on abundance. Significantly higher abundances of bivalve veligers were found at the eastern sites of Algoa East and Woody Cape than at the western sites of Algoa West and Cape Recife at the onshore stations (Figure 2.13), with no such difference among sites at the offshore stations. Depth had a significant effect on the abundance of bivalve veligers (Table 2.4), with statistically higher abundances at the mid and bottom depths than at the surface (Figure 2.14).

Table 2.4: ANOVA examining the effects of Site, Wind, Depth, and Distance on the abundance [$\log_{10}(x+1)$] of bivalve veligers. SS – Sum of Squares; df – degrees of freedom; MS – Mean Squares; F – F-ratio; and p – p-value (significant values are in bold).

Effect	SS	Df	MS	F	p
Site	6,312	3	2,104	9,555	**<0,001**
Wind	0,003	1	0,003	0,014	0,905
Depth	3,151	2	1,576	7,155	**0,001**
Distance	1,867	1	1,867	8,480	**0,004**
Site*Wind	0,157	3	0,052	0,237	0,870
Site*Depth	0,750	6	0,125	0,567	0,756
Wind*Depth	0,102	2	0,051	0,232	0,793
Site*Distance	2,837	3	0,946	4,294	**0,006**
Wind*Distance	0,159	1	0,159	0,721	0,397
Depth*Distance	0,075	2	0,037	0,170	0,844
Site*Wind*Depth	0,283	6	0,047	0,214	0,972
Site*Wind*Distance	1,959	3	0,653	2,965	0,034
Site*Depth*Distance	0,430	6	0,072	0,325	0,923
Wind*Depth*Distance	0,100	2	0,050	0,228	0,796
Site*Wind*Depth*Distance	0,651	6	0,109	0,493	0,813

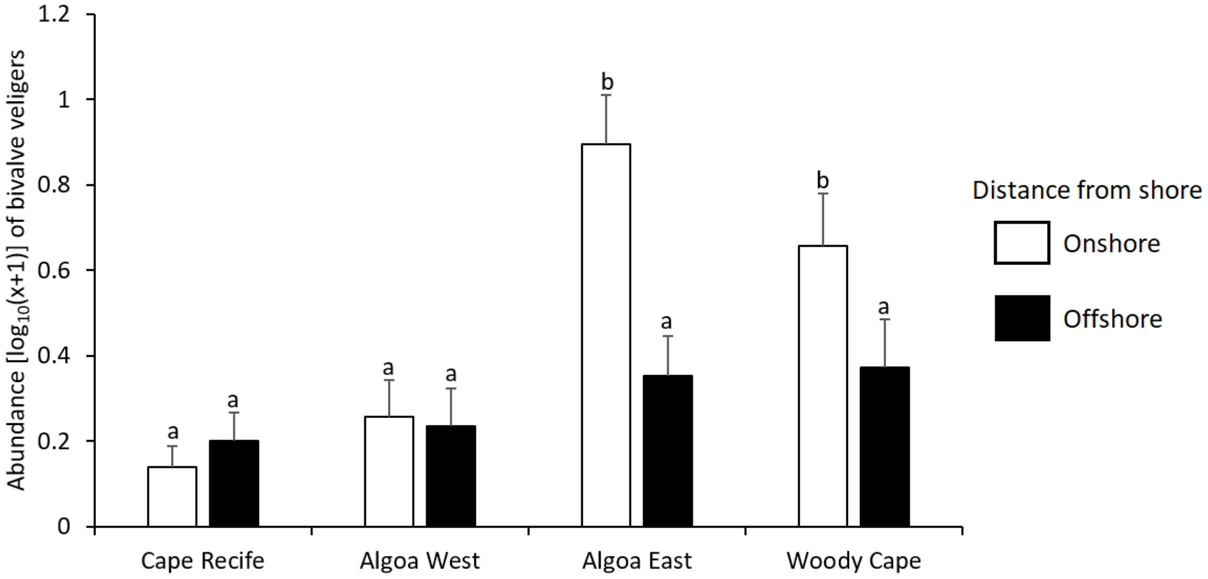

Figure 2.13: Abundance [$\log_{10}(x+1)$] of bivalve veligers with the significant effect of Site and Distance. The letters above the histogram bars indicate homogenous groups across sites per offshore distance identified by a pairwise test performed on the effect of the interaction of Site and Distance. Error bars indicate standard errors.

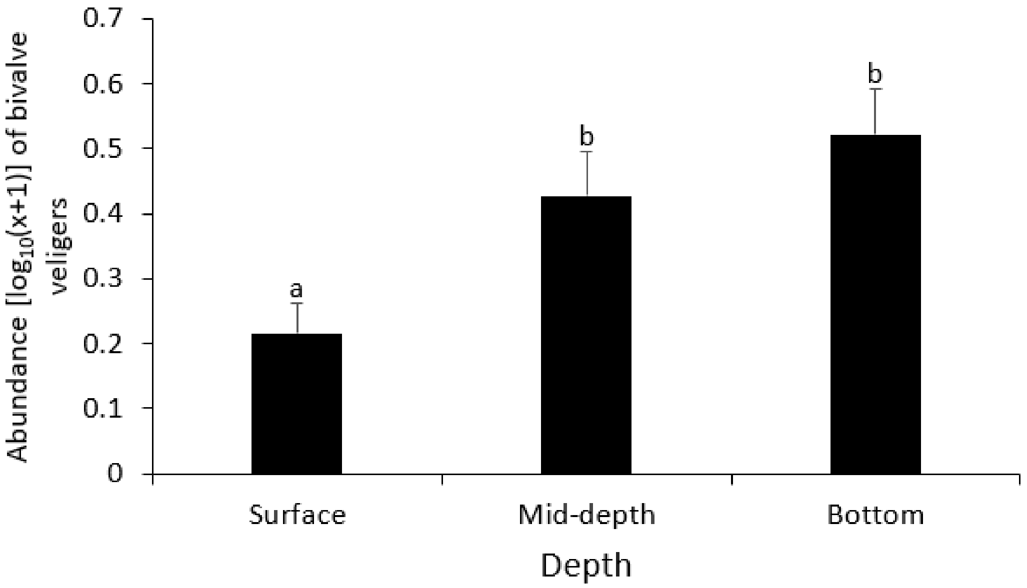

Figure 2.14: Abundance [$\log_{10}(x+1)$] of bivalve veligers with the significant effect of Depth. The letters above the histogram bars indicate homogenous groups across depths identified by a pairwise test. Error bars indicate standard errors.

Brachyuran zoeae

There were significant effects of Depth and Distance as single factors separately (Table 2.5). Significantly greater abundances of larvae were found at the onshore compared to the further offshore station (Figure 2.15). With Depth as a single factor, statistically highest abundances of brachyuran zoeae were found at the mid and bottom depths compared to the surface (Figure 2.16).

Table 2.5: ANOVA examining the effects of Site, Wind, Depth, and Distance on the abundance [$\log_{10}(x+1)$] of brachyuran zoeae. SS – Sum of Squares; df – degrees of freedom; MS – Mean Squares; F – F-ratio; and p – p-value (significant values are in bold).

Effect	SS	Df	MS	F	p
Site	0,778	3	0,259	1,500	0,217
Wind	0,813	1	0,813	4,705	0,032
Depth	12,505	2	6,253	36,178	**<0,001**
Distance	4,132	1	4,132	23,910	**<0,001**
Site*Wind	1,775	3	0,592	3,424	0,019
Site*Depth	1,672	6	0,279	1,612	0,148
Wind*Depth	1,027	2	0,514	2,972	0,054
Site*Distance	1,695	3	0,565	3,268	0,023
Wind*Distance	0,527	1	0,527	3,048	0,083
Depth*Distance	1,734	2	0,867	5,017	0,008
Site*Wind*Depth	0,666	6	0,111	0,642	0,696
Site*Wind*Distance	0,655	3	0,218	1,264	0,289
Site*Depth*Distance	0,593	6	0,099	0,572	0,752
Wind*Depth*Distance	0,222	2	0,111	0,642	0,528
Site*Wind*Depth*Distance	0,513	6	0,085	0,495	0,812
Error	24,888	144	0,173		

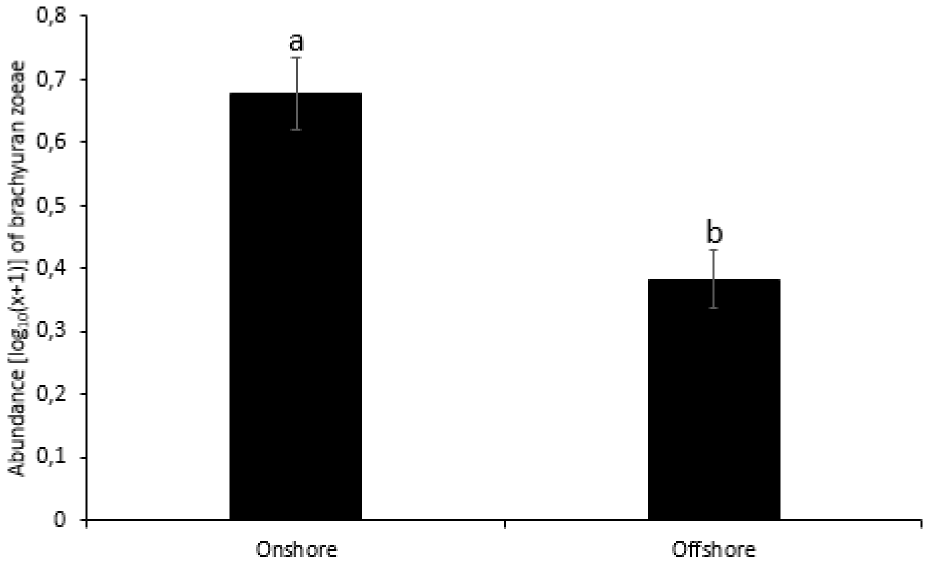

Figure 2.15: Abundance [$\log_{10}(x+1)$] of brachyuran zoeae with the significant effect of Distance. The letters above the the histogram bars indicate homogenous groups across distance identified a pairwise test. Error bars indicate standard errors.

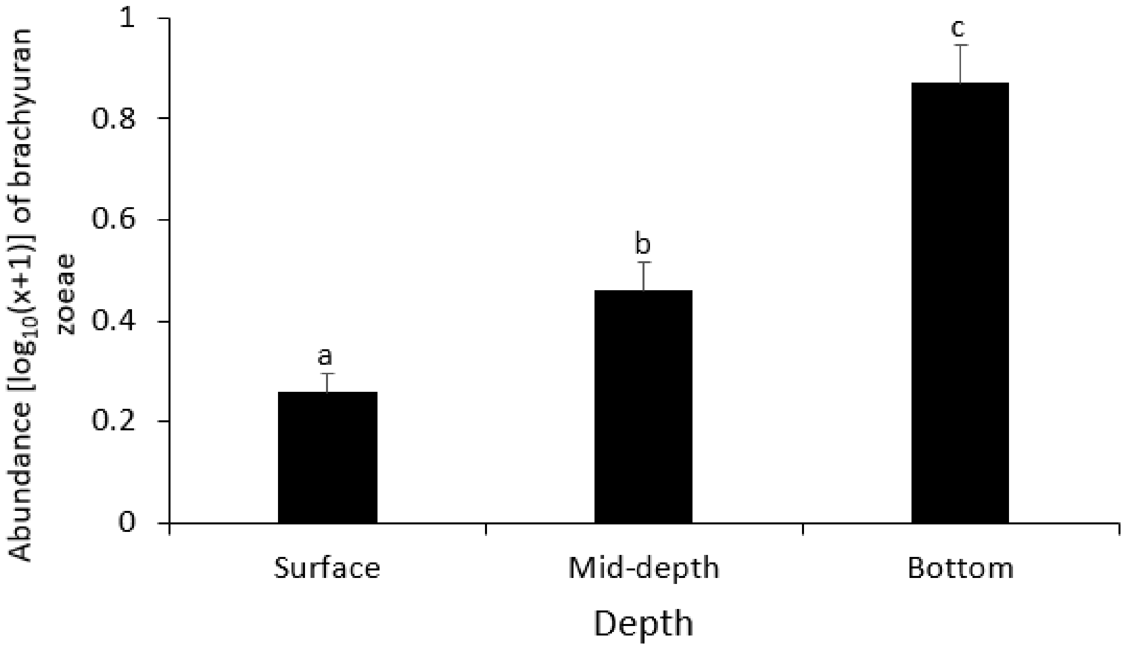

Figure 2.16: Abundance [$\log_{10}(x+1)$] of brachyuran zoeae with the significant effect of Depth. The letters above the histogram bars indicate homogenous groups across depths identified by a pairwise test. Error bars indicate standard errors.

Anomuran zoeae

There was a significant effect of Depth on the abundance of anomuran zoeae (Table 2.6) indicating a change in abundance with depth. Statistically higher abundances were found at mid and bottom depths (Figure 2.17A).

Table 2.6: ANOVA examining the effects of Site, Wind, Depth, and Distance on the abundance [$\log_{10}(x+1)$] of anomuran zoeae. SS – Sum of Squares; df – degrees of freedom; MS – Mean Squares; F – F-ratio; and p – p-value (significant values are in bold).

Effect	SS	Df	MS	F	p
Site	0,189	3	0,063	0,667	0,574
Wind	0,474	1	0,474	5,025	0,027
Depth	10,396	2	5,198	55,110	**<0,001**
Distance	0,037	1	0,037	0,393	0,532
Site*Wind	1,022	3	0,341	3,612	0,015
Site*Depth	1,491	6	0,249	2,635	0,019
Wind*Depth	0,248	2	0,124	1,314	0,272
Site*Distance	0,844	3	0,281	2,984	0,033
Wind*Distance	0,274	1	0,274	2,904	0,091
Depth*Distance	0,580	2	0,290	3,076	0,049
Site*Wind*Depth	0,791	6	0,132	1,399	0,219
Site*Wind*Distance	0,582	3	0,194	2,058	0,108
Site*Depth*Distance	0,760	6	0,127	1,343	0,242
Wind*Depth*Distance	0,228	2	0,114	1,210	0,301
Site*Wind*Depth*Distance	0,685	6	0,114	1,210	0,305
Error	13,583	144	0,094		

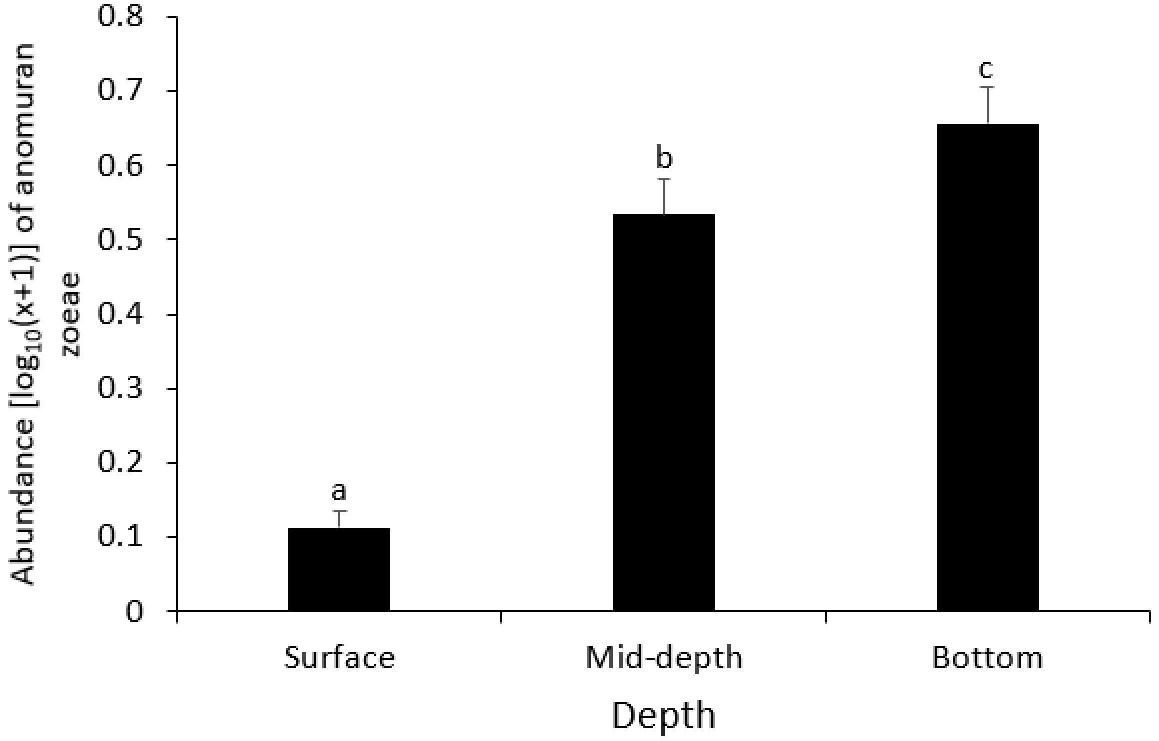

Figure 2.17: Abundance [$\log_{10}(x+1)$] of anomuran zoeae with the significant effect of Depth. The letters above the histogram bars indicate homogenous groups across depths identified by a pairwise test. Error bars indicate standard errors.

Depth had a significant effect on all the taxa, except barnacle nauplii, tested (Tables 2.2–2.6) which could be indicative of a preferred depth at the time of sampling (during the day). For each taxon, significantly lower abundances were recorded in the surface layer of the water column (Figure 2.18).

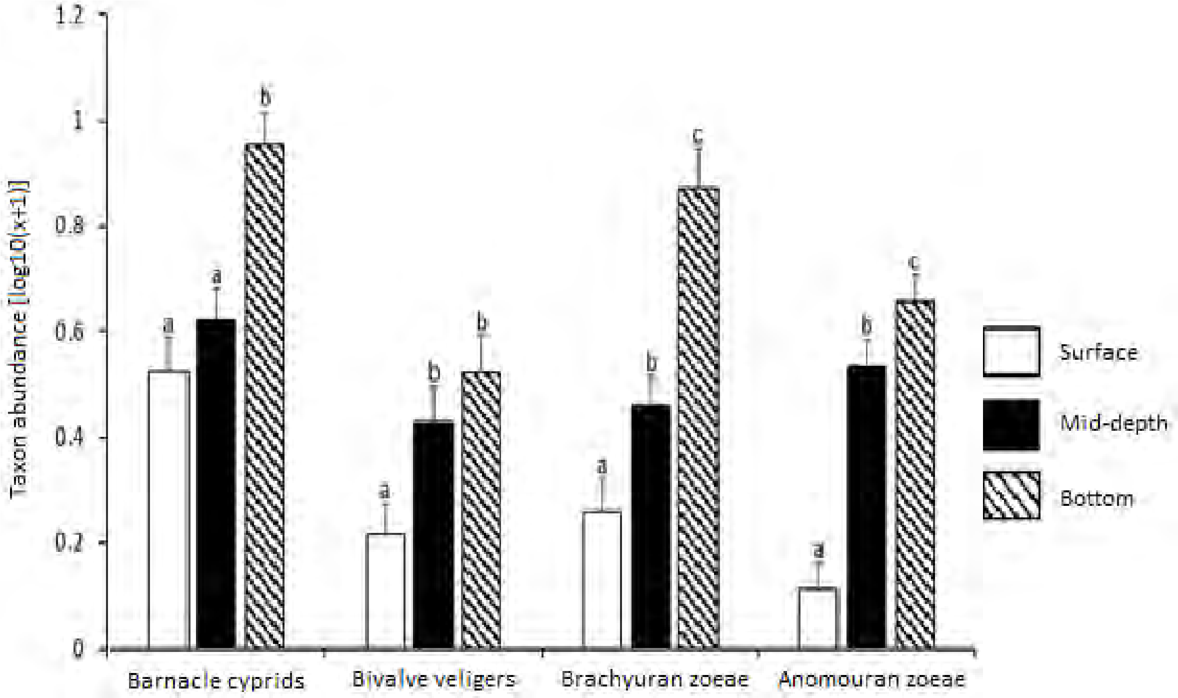

Figure 2.18: Abundance [$\log_{10}(x+1)$] of each taxon with the significant effect Depth. The letters above the histogram bars indicate homogenous groups across depths per taxon identified by pairwise tests performed on the effects of Depth. Error bars indicate standard errors.

At the western sites (CR and AW), easterly winds had an effect on the abundance of barnacle cyprids, brachyuran and anomuran zoeae whilst the same taxa, plus barnacle nauplii, were affected by easterlies on the eastern sites (AE and WC) (Table 2.7). When the wind blew from the east, the abundance of each taxon decreased at the western sites and increased at the eastern sites. Westerly winds had an effect on only two taxa, barnacle cyprids and brachyuran zoeae, with increased abundances at the western sites, and decreased abundances at the eastern sites (Table 2.7). Depth had a significant effect on all the taxa examined, with barnacle nauplii abundances being higher at mid-depths, whilst barnacle cyprids, brachyuran and anomuran zoeae showed higher abundances at the bottom, and bivalve veliger abundances were higher at both mid-depth and at the bottom (Table 2.7 and Figure 2.18).

Table 2.7: Summary table showing the effects of wind and depth on each taxon from either side of the bay. The upward pointing arrows indicate increased abundances and the downward pointing arrows indicate decreased abundances. CR – Cape Recife, AW – Algoa West, AE – Algoa East and WC – Woody Cape. No - no change in the abundance of organisms, Yes – a change in the abundance of organisms and ns – no significant effect of a factor.

Taxon	West sites (CR & AW)		East sites (AE & WC)		Depth
	Easterly wind	Westerly wind	Easterly wind	Westerly wind	
Barnacle cyprids	Yes ↓	Yes ↑	Yes ↑	Yes ↓	Yes, bottom
Bivalve veligers	ns	ns	ns	Ns	Yes, mid-depth & bottom
Brachyuran zoeae	Yes ↓	Yes ↑	Yes ↑	Yes ↓	Yes, bottom
Anomuran zoeae	Yes ↓	No	Yes ↑	No	Yes, bottom

2.3.3 Bio-physical relationships

Multiple Regression

Out of 239 models, 159 models were significant with an alpha value of 0.05. After applying the Benjamini-Hochberg false discovery calculation, the new cut off value for significance was 0.0265 (Appendix, Table A2). Only the models with the highest explanatorypower, based on the AIC value, for each taxon are shown (Table 2.8). Meridional flow, with a lag period of three days, had the strongest explanatory power of 12.3% for barnacle nauplii abundances (AIC = 331.16) and the dissipation of turbulent kinetic energy at a 4-day time lag had the highest explanatory power of 9.1% for barnacle cyprid abundances (AIC = 271.573). Bivalve veliger abundances (AIC = 267.71), were better explained (13.4%) by the dissipation of kinetic energy at a 1-day time lag. Brachyuran zoeae abundances were better exaplained (15.2%) by a combination of zonal flow and the dissipation of turbulent kinetic energy at a 7-day time lag (AIC = 277.689). The combination of the dissipation of turbulent kinetic energy and zonal flow explained 31.4% of anomuran zoeae abundances at a 7-day time lag (AIC = 136.642) Regardless of which lag period best explained the abundance of each taxon, they all related positively to the environmental variables (Table 2.8).

Table 2.8: Multiple linear regression analyses showing the best variable/model for each taxon abundance tested over eight time-lags. For each variable/model, the sign of the relationship, the level of significance, the total variation explained, and the AIC information are shown. AIC indicates the Akaike Information Criterion.

Species	Variable	Sign	Lag period	p-value	R^2	AIC
Barnacle nauplii	Meridional flow	+	3 days	<0.001	0.123	331.16
Barnacle cyprids	Dissipation of turbulent kinetic energy	+	4 days	<0.001	0.091	271.573
Bivalve veligers	Dissipation of turbulent kinetic energy	+	1 day	<0.001	0.134	267.71
Brachyuran zoeae	Dissipation of turbulent kinetic energy & Zonal flow	+	7 days	<0.001	0.152	277.689
Anomuran zoeae	Dissipation of turbulent kinetic energy & Zonal flow	+	7 days	<0.001	0.314	136.642

Distance-based Linear Modelling

The relationships between total larval abundance [$\log_{10}(x+1)$] and environmental variables (upwelling index, turbulent kinetic energy, zonal and meridional flow, fluorescence, oxygen, pH and temperature) were investigated using Distance-based Linear Models (DistLM). The results of the marginal tests revealed a significant relationship between total larval abundance and upwelling index, dissipation of turbulent kinetic energy, fluorescence, oxygen and pH, for both the R^2 and the AIC model selection procedures (Table 2.9).

Table 2.9: Marginal test results for the distance-based linear modelling (DistLM) using the Best Selection Procedure and 999 permutations, examining eight factors with the R^2 and the AIC model selection. SS(trace) = Sum of Squares, Pseudo-F = multivariate analogue to Fisher's F test, p = level of significance and Prop. = proportion of variation explained. Significant values are shown in bold.

Selection criterion	Variable	SS(trace)	Pseudo-F	P	Prop.
R^2	Upwelling	3490,7	4,0979	**0,01**	2,11E-02
	Dissipation of turbulent kinetic energy	15057	19,037	**0,001**	9,11E-02
	Zonal flow	1255,5	1,4538	0,202	7,59E-03
	Meridional flow	1876,4	2,181	0,11	1,13E-02
	Temperature	1355,1	1,5701	0,206	8,20E-03
	Fluorescence	6313,9	7,5437	**0,001**	3,82E-02
	Oxygen	4225,6	4,9832	**0,006**	2,56E-02
	pH	7148,5	8,586	**0,001**	4,32E-02
AIC	Upwelling	3490,7	4,0979	**0,012**	2,11E-02
	Dissipation of turbulent kinetic energy	15057	19,037	**0,001**	9,11E-02
	Zonal flow	1255,5	1,4538	0,221	7,59E-03
	Meridional flow	1876,4	2,181	0,102	1,13E-02
	Temperature	1355,1	1,5701	0,184	8,20E-03
	Fluorescence	6313,9	7,5437	**0,001**	3,82E-02
	Oxygen	4225,6	4,9832	**0,006**	2,56E-02
	pH	7148,5	8,586	**0,001**	4,32E-02

The best model, however, from the R^2 model selection procedure included a combination of all the environmental factors (upwelling index, dissipation of turbulent kinetic energy, zonal and meridional flows, temperature, fluorescence, oxygen and pH) investigated, explaining 20% of the total variation, whilst five (upwelling index, dissipation of turbulent kinetic energy, fluorescence, oxygen and pH) explained the highest variation (19%) when using the AIC model selection procedure (Table 2.10).

Table 2.10: Overall BEST DistLM procedure examining the relationship between environmental variables and the total larval abundance in the water column using the R^2 and the AIC model selections. R^2 = total variation explained, RSS = Residual Sum of Squares and AIC = Akaike Information Criterion.

Selection	Variables	R^2	RSS	AIC
R^2	Upwelling Dissipation of turbulent kinetic energy Zonal flow Meridional flow Temperature Fluorescence Oxygen pH	0,201	1,32E+05	
AIC	Upwelling Dissipation of turbulent kinetic energy Fluorescence Oxygen pH	0,19	1,34E+05	1269

Distance based Redundancy Analysis (dbRDA) plots were generated to visually display the direction and strength of the relationship between the total larval abundance and the environmental variables, which best explained the total variation for both (R^2 and AIC) model selection procedures (Figure 2.19). The total variation explained by the first two axes were aprroximately 18% and 17% for the R^2 and AIC model procedures, respectively (Figure 2.19).

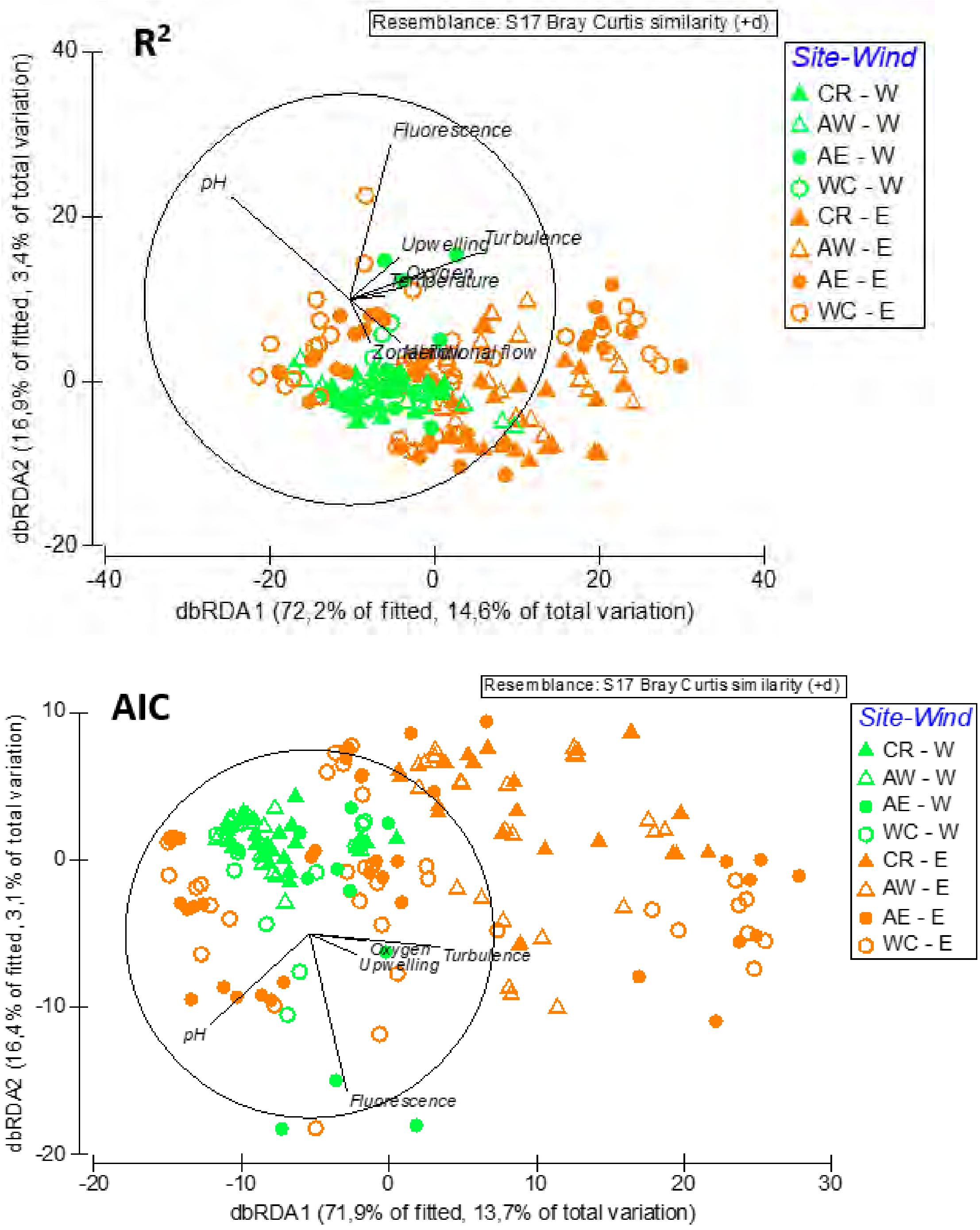

Figure 2.19: Distance-based Redundancy Analysis (dbRDA) plot showing the relationship between total larval abundance and environmental variables according to the site and wind interaction. Vector lines represent the different environmental variables most important to each modelling approach. The length and direction of the vector lines indicate the strength and direction of the relationship, and percentages on the x- and y-axis indicate the total variation explained by each axis.

2.4 Discussion

All the larvae collected during this study generally avoided the surface, with increased abundances at depths below the surface and closer to the bottom. This trend was expected, as sampling was done during the day, when most larvae tend to inhabit the deeper layers of the water column, with an ascent during the night; this phenomenon is called diel vertical migration (Shanks & Brink, 2005; dos Santos *et al.*, 2007). This phenomenon is common in zooplankton (Lampert, 1989; Dodson, 1990; Cohen & Forward Jr, 2009; Brierley, 2014; Daase *et al.*, 2016; Tutasi & Escribano, 2020; Kuzenkov *et al.*, 2021) and has been observed for decapod larvae (Marta-Almeida *et al.*, 2006; dos Santos *et al.*, 2008; Brown *et al.*, 2014), barnacle nauplii (Tapia *et al.*, 2010; Bonicelli *et al.*, 2016), bivalve veligers (Tremblay & Sinclair, 1990a, b; Bonicelli *et al.*, 2016) and the postflexion stages of fish species (Brewer & Kleppel, 1986). Some aquatic species however, such as the larvae of the estuarine crab *Parasesarma catenatum* inhabit the surface layers during the day (positively phototactic) (Lago, 1988), while others, such as the zoeae of the fiddler crab *Uca pugilator*, swim up and down the water column, following an ebb or flow tide (López-Duarte & Tankersley, 2007).

Irrespective of the cue that larvae respond to, diel vertical migration is initiated to either maximise feeding (Huntley & Brooks, 1982; Wroblewski & Richman, 1987 Lampert, 1989, Raby *et al.*, 1994), escape visually feeding predators (Dodson, 1990), and/or to enhance nearshore retention of larvae (Marta-Almeida *et al.*, 2006; Naylor, 2006; dos Santos *et al.*, 2008) thereby keeping larvae under favourable ecological conditions (Naylor, 2006).

As shown by both the multiple linear regressions and distance based linear modelling, larval abundances had strong positive, relationships with the environmental variables. The positive relationship between taxa with along- and crosshore currents might result in an onshore movement of species due to the nature of the bay, whereby north and westerly movements are in an onshore direction (Largier, 2020; Satterthwaite *et al*., 2021). Similarly, a positive relationship with upwelling, especially for bottom dwelling organisms, might result in inshore advection (Satterthwaite *et al*., 2021). A relationship with zonal flow signifies a west to east movement of taxa, whilst a relationship with fluorescence, dissipation of turbulent kinetic energy, oxygen and pH could indicate a change in distribution by depth in taxon abundances, as these factors can vary accordingly (Lampert, 1989). Fluorescence, dissolved oxygen, and pH decreased with depth, as indicated by the CTD measures (data not shown), and as shown by the turbulent kinetic energy equation, dissipation of turbulent kinetic energy decreased with depth (Pringle, 2007).

Light plays a fundamental role in photosynthesis (Barber, 2017) and its penetration in the water column decreases with depth in open oceans (Ackleson, 2003), resulting in a vertical gradient of chlorophyll (Dodson, 1990) and oxygen (Barber, 2017). In very shallow coastal areas, however, as in this study, light is acknowledged to penetrate to the seafloor, resulting in maximum primary production at the seabed (Ackleson, 2003; Gattuso *et al*., 2006). This implies that regardless of whether or not larvae were closer to the surface or the bottom layer, they were likely exposed to more-or-less equal feeding opportunities, but those at the surface might be assumed to be more exposed to visual predators. The dbRDA plots show that during westerly winds, larval abundance was mostly negatively related to fluorescence. Fluorescence decreases with depth, especially in the open ocean (Steele & Yentsch, 1960; Sauzéde *et al*., 2015); in shallow water systems, however, more than half of all profiles can reveal a vertically homogenous chlorophyll distribution (Zhao *et al*., 2019). In this study, 37.2% of the measurements had a homogenous distribution of chlorophyll, 32.8% showed a decrease in chlorophyll distribution with depth, 25% recorded a higher chlorophyll distribution in the mid-depths and 5% showed an increase in chlorophyll with depth during all the 64 sampling periods (data not shown). While acknowledging the pooling of larvae from differnet taxa, given the overall very shallow depths sampled, the fact that most larvae mostly inhabited the bottom layers could therefore be attributed to escaping visual predators rather than being related to feeding, as only 5% of the whole data set showed that chlorophyll was high at the bottom. With the highest percentage of profiles showing homogenous chlorophyll distribution throughout the water column and considering the generally very shallow depths, it is unlikely that larvae at the bottom would starve, especially considering the homogenous mixing in very shallow water systems as a result of wind and tidal action (Kjerfve & Magill, 1989).

Wind speeds increased from the morning, peaked around midday, and slowed during the evenings, which led to increased dissipation of turbulent kinetic energy during the day, rather than at night and, depending on the wind direction, led to increased upwelling (with easterly winds) or downwelling (with westerly winds). Its long been acknowledged that larvae respond to increased dissipation of turbulent kinetic energy by either sinking or ascending through the water column (Crisp, 1955; Fuchs *et al.*, 2007; 2010; 2017). Abundances of barnacle cyprids, and brachyuran zoeae were positively related to a combination of upwelling and dissipation of turbulent kinetic energy (Fuchs *et al.*, 2010) with a 1-day lag (Fuchs *et al.*, 2010), suggesting a relatively quick response to the hydrographic variables. Although not directly associated with dissipation of turbulent kinetic energy, barnacle cyprids and decapod zoeae have been noted to descend to bottom water layers during the day, and to ascend to the surface water layer at the night (dos Santos *et al.*, 2007; 2008). The sinking behaviour with increased dissipation of turbulent kinetic energy in an upwelling system enhances the likelihood of nearshore advection/confinement of larvae (Marta-Almeida *et al.*, 2006), thereby contributing to increased larval retention along the coast near the parental/adult population (Fuchs, *et al*., 2010).

A relationship between larval abundances and zonal flow within a bay means that larvae will still move onshore in either direction (west or east) as the headlands typically protrude on either side of an embayment, although the headland in this study area, Algoa Bay, is more pronounced on the western side. The positive relationships of barnacle nauplii with meridional flow is suggestive of increased larval retention within the bay. Although there was no relationship between barnacle nauplii and cyprids and bivalve veligers with zonal flow, the patterns in Figures 2.9, and 2.11 and 2.13 show that easterly wind resulted in increased abundances of barnacle nauplii, bivalve veligers at the eastern rather than the western sides of the bay and westerly winds resulted in increased cyprid abundances at the western side. On the other hand, abundances of barnacle cyprids a were greater on the western side of the bay after westerly wind events. Despite the general similarity in circulation between the western and eastern section of the Algoa Bay (Schumann *et al.,* 2005), cyclonic and anti-cyclonic gyres occurring in bays (Monteiro & Roychoudhury, 2005; Dubois *et al*., 2007) may explain the increased abundances of taxa at the eastern sites during easterly winds, and at the western sites during westerly events, as this pattern was shown by all the taxa. North-easterly winds, combined with the topography of a bay, result in an anti-cyclonic gyre on the western side of the bay and easterly flowing currents within the bay (Goschen & Schumann, 2011). The east moving current and the direction of the Agulhas current in this study could result in a cyclonic gyre on the eastern side of the bay. Although the general direction of the current flow was in the direction of the wind (Goschen & Schumann, 1988; 2011), currents in Algoa bay sometimes move in opposite directions to the wind direction (Goschen & Schumann, 1988), thereby most likely transporting larvae in the opposite directions to the wind. This phenomenon of opposing current and wind direction, however, was not observed in the bay during the sampling periods.

With easterly winds inducing upwelling in this region (Schumann *et al.*, 1988), and larvae weakly, yet positively related to fluorescence, westerly winds could potentially transport larvae from Cape Recife into Algoa bay, and easterly winds could transport larvae from food-rich Woody Cape into Algoa bay. This suggests that westerly winds moving nutrient rich upwelled waters from Cape Recife into the bay (Goschen & Schumann, 1995) might have resulted in the increase in abundances on the western sector of the bay. Similarly, in another study, easterly winds bringing the nutrient rich upwelled waters from Cape Padrone into the bay (Goschen *et al.*, 2012) might have resulted in an increase in larval abundances in the eastern sector of the bay. In this case, larvae would have been trapped in the gyres produced on either side of the bay. Additionally, larvae spawned/found in the bay are most likely to remain within the bay (Dubois *et al.*, 2007; Banas *et al.*, 2009; Morgan *et al.*, 2011), especially in Algoa bay, which has little freshwater input (Schumann *et al.*, 2005) and therefore less flushing of water outside the bay.

The proposed hypothesis, that larvae are transported eastwards by westerly winds and westwards by easterly winds cannot be accepted uncritically. Evidence from this study shows that larval abundances increased on the eastern side of the bay during easterly winds and on the western side of the bay during westerly winds. A sampling plan whereby all sides of the bay are sampled at the same time would give a better and more conclusive result. Without such a sampling plan, one cannot draw unequivocal conclusions on the overall effects of wind on the transport of larvae in the entire bay.

Chapter 3

The effect of wind direction on the settlement and recruitment of invertebrate larvae on the south-east coast of South Africa

3.1. Introduction

Dispersing larvae of sessile/sedentary species are morphologically and ecologically different from their adult forms (Hill, 1991; Nielsen, 1998) and, as planktonic organisms, their dispersal is controlled by a combination of physical and biological processes (Thorson, 1950; Hill, 1991; Natunewicz & Epifanio, 2001; Cowen & Sponaugle, 2009; Coelho & Lasker, 2016). Dispersal of larvae depends largely on the time they spend in the water column (Jenkins & Hawkins, 2003; Shanks *et al.*, 2003; Einfeldt *et al.*, 2017; Bashevkin *et al.*, 2020) and this dispersal offers a range of ecological benefits to both population and community (Strathmann, 1974; Miyake *et al.*, 2017; Alfaya *et al.*, 2020).

Dispersal increases the opportunity to escape local benthic extinction resulting from deteriorating local conditions, reduces intra- and interspecific competition for resources with adults, decreases inbreeding, and increases distributional range, allowing the colonization of new, more favourable habitats (Strathmann & Strathmann, 1982; Prince *et al.*, 1987; Petersen & Svane, 1995; Pechenik, 1999; Jenkins & Hawkins, 2003; Miller & Morgan, 2014; Bonel *et al.*, 2020). Reproductive output and rate, larval dispersal and mortality rates are the cornerstones of population size, distribution and community connectivity (Gaines & Roughgarden, 1987; Minchinton & Scheibling, 1991; Porri *et al.*, 2008; Cowen & Sponaugle, 2009; Connolly & Baird, 2010).

The completion of a successful biphasic life cycle involves the return and settlement of propagules to a suitable benthic habitat, followed by further development to become fertile adults (Pineda, 1994; 2000; Abelson & Denny, 1997; Wendt & Woollacott, 1999; Hadfield & Paul, 2001). The process whereby pelagic larvae leave the water column for the benthos, attach to a substratum and undergo metamorphosis is referred to as settlement (Hadfield & Paul, 2001), and a high degree of temporal and spatial variation in this process (Gaines &

Roughgarden, 1985; 1987; Roughgarden *et al.*, 1988; Rodríguez *et al.*, 1993; Garcia *et al.*, 2003; Porri *et al.*, 2006a; Raabe & Gilg, 2020) appears to be the rule rather than the exception (Marshall & Keough, 2003). Differences in reproductive output, larval transport mechanisms, mortality and distribution of larvae whilst in the water column play a major role in the episodic nature of settlement (Gaines & Roughgarden, 1987; Minchinton & Scheibling, 1991; Morgan *et al.*, 2011) and are critical factors in the structuring of benthic communities (Thorson, 1950; Gaines & Roughgarden, 1985; Bertness *et al.*, 1996; Dixon *et al.*, 1999; Connolly & Baird, 2010; Morgan *et al.*, 2011).

For species with a biphasic life history, population dynamics are largely regulated by larval supply, settlement and recruitment (Olivier *et al.*, 2000; Morgan *et al.*, 2011), which are in turn strongly affected by variability in the scales of larval dispersal (Jenkins & Hawkins, 2003). For larval dispersal and distribution within the water, physical processes are important drivers (Walters *et al.*, 1996; Qian, 1999; Faimali *et al.*, 2004). These physical processes vary at different spatial and temporal scales, especially due to wind forcing (Sverdrup, 1947; Gill & Clarke, 1974; Philander & Pacanowski, 1981; Schumann *et al.*, 1982; Muraleedharan & Kumar, 1996; Sydeman *et al.*, 2014). Wind therefore, directly or indirectly, affects many components of final recruitment, such as larval dispersal and supply, and thus settlement rates.

Spatio-temporal variation in wind regimes (Caldwell *et al.*, 1986; Schumann & Martin 1991) results in different oceanic dynamics (Lighthill, 1969), thereby influencing settlement patterns. Among oceanographic processes driven by wind, upwelling and dissipation of turbulent kinetic energy play a key role in larval transport, distribution and delivery (Roughgarden *et al.*, 1988; Marta-Almeida *et al.*, 2006). Upwelling is responsible for transporting surface-dwelling larvae offshore, whilst downwelling transports these surface-dwelling larvae onshore (Roughgarden *et al.*, 1988). Conversely, bottom-dwelling larvae are transported onshore during an upwelling event, while downwelling results in offshore transport (Marta-Almeida *et al.*, 2006). Onshore transport of larvae may increase the chances of settlement of competent larvae through contact with benthic substrata on the coast. Wind-induced turbulence is also responsible for variability in settlement through increased encounter rates with substrata (Abelson & Denny, 1997).

Larvae of marine benthic communities settle on soft and/or hard substrata (Bayne, 1964; Rodríguez *et al.*, 1993; Pineda, 1994; Munday, 2002; Cowen & Sponaugle, 2009) including rocky shores. Barnacles and bivalves often dominate the rocky intertidal zone (Broitman *et al.*, 2001; Branch & Branch, 2018); depending on the shore height, two species of mussels, *Perna perna* and *Mytilus galloprovincialis*, dominate the south coast of South Africa (Erlandsson *et al.*, 2006; Porri *et al.*, 2007; Zardi *et al.*, 2007).

The aim of this study was to investigate the effects of the predominant westerly (dominant in winter) and easterly (dominant in summer) winds of the south coast of Algoa Bay (Goschen & Schumann, 1995) on the settlement and recruitment of the two dominant mussel species, *Perna perna* and *Mytilus galloprovincialis*, and barnacle cyprids. Settlement in this context was defined as the process (reversible for mussels, or irreversible for barnacles) of initial attachment of larvae onto substrata (Bayne, 1964; Keough & Downes, 1982). Depending on the taxon, larvae arriving onshore may or may not undergo metamorphosis (Seed & Suchanek, 1992), but for all groups, settlement is the transition from a planktonic to a benthic stage (Rodriguez *et al.*, 1993; Poulin *et al.*, 2002). Recruits, on the other hand, were defined as individuals that had survived post-settlement mortality and had remained on the shore for an arbitrarily defined, but relatively brief, period of time after settling (Connell, 1985; Rodriguez *et al.*, 1993).

Nearshore ocean current circulation is the main driver of the horizontal movement of invertebrate larvae in the water column (Pfaff *et al*., 2015). Wind speed and direction are said to be some of the main drivers of current speed and direction (Bressan & Constantin, 2019; Constantin, 2021). My hypothesis, therefore, for this section of the study, was that seasonality in wind structure would be an important regulator of settlement and recruitment. I hypothesized that increased speed and frequency of westerly winds would result in increased settlement, as the currents would be moving onshore (currents moving at an angle, to the left of the wind direction) and increased speed and frequency of easterly winds would result in offshore moving currents which would transport larvae offshore (Marta-Almeida *et al*., 2006).

3.2. Materials and Methods

3.2.1. Study sites

The study was conducted at six sites on the south east coast of South Africa (Figure 3.1): Skoenmakerskop (SK; -34°02’ S, 25°32’ E), Chelsea Point (CP; -34°02’ S, 25°34’ E), Boardwalk (BDW; -33°58’ S, 25°39’ E), Brighton Beach (BB; -33°53’ S, 25°37’ E), Cannon Rocks (CR; -33°45’07” S, 26°32’ E), and Kenton-on-Sea (KOS; -33°41’ S, 26°40’ E). The coast, (and associated sites), lies roughly in a south-west (SW) to north-east (NE) direction west-east, which is parallel to the prevailing winds in the region (Schumann & Martin, 1991) (Figure 3.1). SK and CP are located on the open coast west of the bay, while BDW and BB are located within Algoa Bay, and CR and KOS are located on the open coast to the east of the bay.

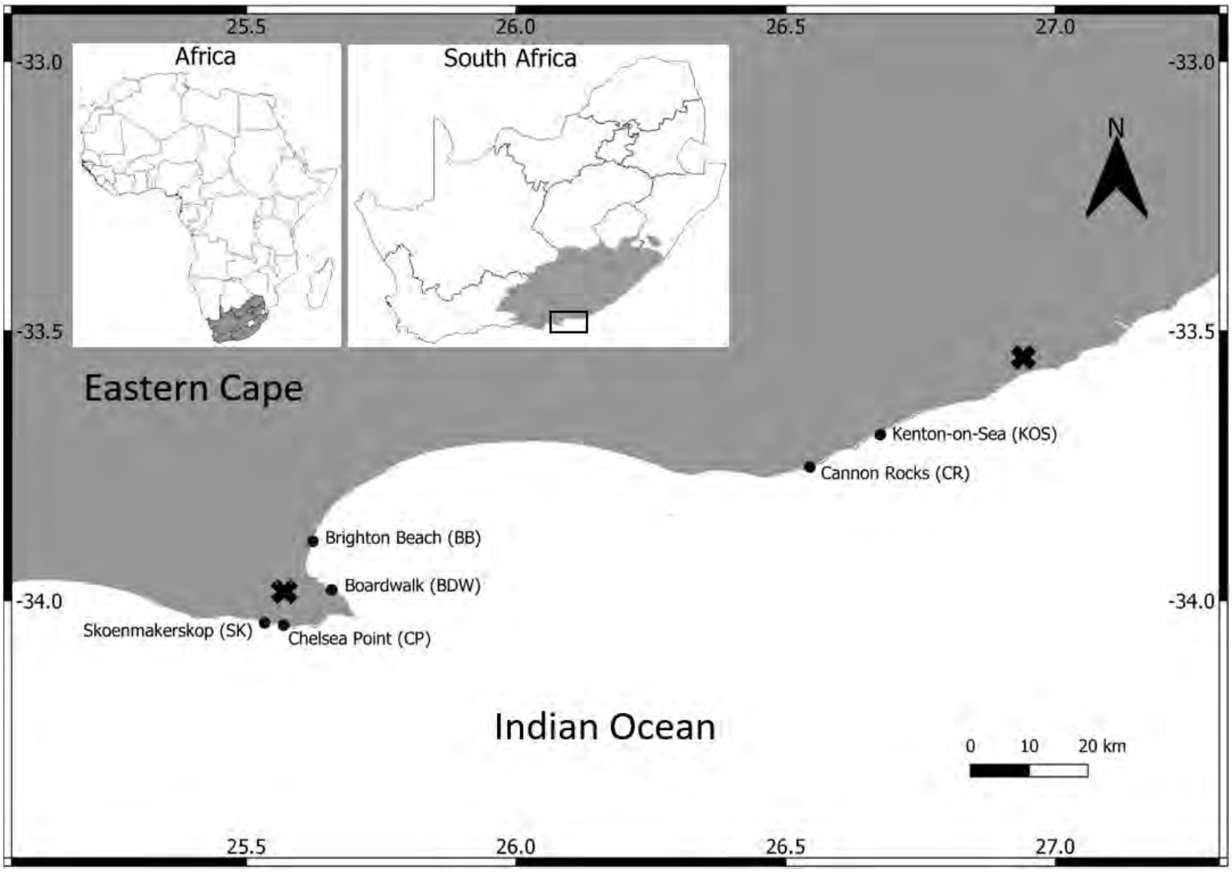

Figure 3.1: Map of the sampling sites (black dots) along the south east coast of South Africa. The black crosses represent the Port Elizabeth (left) and the Port Alfred (right) anemometer locations.

3.2.2. Physical data

Hourly along- and crosshore wind speed covering the whole sampling months were obtained from ERA5 hourly data on single levels from 1940 to present website (see previous chapter for details). The pixels of the data points for wind speed were extracted in respect to the coordinates of the sampling sites. Due to the distance between adjacent sites, and the size of the pixels (which covered two adjacent sites), the same coordinates from a given pixel were used for adjacent sites (e.g. Skoenmakerskop and Chelsea Point; Boardwalk and Brighton Beach; and Cannon Rocks and Kenton-on-Sea had similar co-ordinates in terms of wind data from the pixels). Hourly wind direction data were then calculated using the proxy of wind speed (zonal and meridional) on R-studio version 2002.02.3. The equation is as follows:

*Wind direction = function(u,v){(180+atan2(u,v)*180/pi)%%360}*

Where *u* is the alongshore wind speed, *v* is the cross-shore wind speed, *atan2* returns the angle in radians for the tangent *u*/*v*, and *pi* is the items response probability.

Dissipation of turbulent kinetic energy (Wkg^{-1}) was calculated following Pringle (2007) and the upwelling index ($m^3km^{-1}s^{-1}$) was calculated using the equation by Oakey (1985) as described in Chapter Two.

3.2.3. Biological data

Plastic kitchen scouring pads (approx. 10–11 cm in diameter) were used as an artificial settlement substratum for mussel larvae, as has been used by many researchers (Gilg & Hilbish, 2000; Connolly *et al.*, 2001; Smith & Rule, 2002; Porri *et al.*, 2006a, b; 2007; Bownes *et al.*, 2008; Bownes & McQuaid, 2009; von der Meden *et al.*, 2012). At each site, a maximum of ten scouring pads were attached using cable ties to pre-drilled set eyebolts placed within mussel beds on the rocky shore. To ensure independence of each pad, eye-bolts were placed at least 50 cm apart. Due to losses of the scouring pads and eyebolts, the exact positions of the pads differed throughout the study, as continuous maintenance re-drilling and then re-positioning of collectors was necessary. Settlement and recruitment were measured monthly from May 2017 to June 2018 during spring, at full moon low tides. All the collectors were deployed and replaced monthly at each site, and each was individually stored in jars with 90–100% ethanol. The preserved collectors were transported to the laboratory at the Aquatic Ecophysiology Research Platform (AERP), within the South African Institute for Aquatic Biodiversity (SAIAB), for further processing.

Simultaneously, barnacle settlement/recruitment was monitored using 10 x 10 x 0.8 cm (height x width x thickness) PVC plastic settling plates coated with 7 x 10 cm (height x width) sandpaper (a rubbery, uniformly rough-textured surface), following Farrell *et al*. (1991); Menge (2000) and Shanks (2009a, b). Each plate was fastened tightly to the rock surface using a stainless-steel screw through a predrilled hole on the edge of the PVC, but not the sandpaper. Plates were also replaced on a monthly basis. At collection, plates were individually put in separate plastic bags and transported to the SAIAB laboratory freezer for later processing and the determination of barnacle cyprid and juvenile/spat abundances.

The scouring pads were washed to remove any bivalve settlers and/or recruits that had attached over each month of deployment. The washing process included soaking each collector individually in 3.5% sodium hypochlorite solution, to detach bivalves from the substratum by dissolving the byssal threads (Pearce & Bourget, 1996; Connolly *et al.*, 2001). Each pad was then individually rinsed with fresh water, removing all particles found on them (including mussel settlers and recruits). The debris-filled liquid was then filtered through a 75 µm sieve. The resulting contents from the sieve were then viewed under a Zeiss (Stemi DV4) dissecting microscope. Only the most abundant mussel species that occur on the stretch of coast targeted by the study were considered, which were *Perna perna* (the indigenous brown mussel) and *Mytillus galloprovincialis* (the invasive Mediterranean mussel) (Branch *et al.*, 2010). Species were identified, counted and measured using an ocular micrometer on the dissecting microscope. Mussels of ≤ 360 µm were referred to as settlers and their arrival time on the shore was assumed to be at most 2 days prior to collection (Porri *et al.*, 2006b) while mussels of > 360 µm were presumed to have been settled on the shore for more than 2 days (Bayne, 1964; Bownes *et al.*, 2008), and were therefore referred to as recruits. Data for the two size classes were analysed separately. Similarly, barnacle cyprids are known to take between 24 hours (Thiyagarajan & Qian, 2008) and 2 days for metamorphosis to be fully completed and to become juveniles (Essock-Burns *et al.*, 2017), and therefore abundance data for cyprids and juveniles were also analysed separately.

3.2.4. Statistical analyses

Hourly wind data are shown as wind rose plots created in Oriana v. 4.01 for all the sampling sites (Figures 3.2–3.5).

The directions of the bars on the plots represent the direction from which the wind was blowing. The wind data used in the plots were those recorded retrieved from the ERA5 hourly data on single levels from 1940 to present website for the total period from the day the scouring pads and barnacle plates were placed on the rocky shores to the day they were removed. In the correlation analysis however, different time scales were used to account for the different expected times of arrival for settlers and recruits, respectively.

Normality of data was tested using the Shapiro-Wilk test. Levene's test was selected for its power and robustness in checking homogeneity of variances (Carroll & Schneider, 1985; Lim & Loh, 1996; Gastwirth *et al.*, 2009). Homogeneity of variances was achieved by transforming raw data using [$\text{Log}_{10}(x+1)$]. To determine larval settlement patterns, a 2-way analysis of variance (ANOVA) was performed to test the effects of Site (6 levels, fixed), and Month (fixed, 14 months). Following significant effects of any factor or interaction on abundances, post-hoc Fisher LSD contrast tests were performed. In addition to each taxon and ontogenetic stage being analysed separately, the total settlers from each species (*Perna perna* and *Mytilus galloprovincialis*) were pooled and analysed, and the same process was followed with recruits. Due to multiple tests being performed, Benjamini-Hochberg corrections were applied to reduce the occurrence of a Type I error (False Discorvery Rate- FDR, Benjamini and Hochberg, 1995). Statistical analyses were performed using Statistica 13.2.

Multiple regression analyses were performed to test for possible relationships between the abundance of each developmental stage of each taxon (settlers and recruits for mussels, cyprids and juveniles for barnacles) and the physical variables of dissipation of turbulent kinetic energy and upwelling. Barnacle cyprids take about 24 hours (Thiyagarajan & Qian, 2008) to 2 days for full metamorphosis, to then become juveniles (Essock-Burns *et al.*, 2017). Bivalve settlers were deemed to be organisms ≤ 360 µm and which were on the collecting pad for a maximum of 2 days, and those deemed to have settled for longer and were > 360 µm were referred to as recruits (Porri *et al.*, 2006b). Due to temporal differences in the conditions which each ontogenetic stage experienced, lag periods differed for the different ontogenetic stages in the analyses. Dissipation of turbulent kinetic energy and upwelling were therefore lagged for 12 hours, 24 hours, and 2 days for settlers and cyprids, and 24 hours, 2 days, 4 days, 7 days, and 1 month for mussel recruits and juvenile barnacles, repectively. In addition to these multiple regressions, correlation analyses were done to test for possible relationships between the number of hours of westerly and easterly winds and the abundances of mussel settlers and recruits, as well as cyprids, and juvenile barnacles. The lag periods used for this last set of correlations were the 1same as for dissipation of turbulent kinetic energy and upwelling. Due to the multiple tests performed, the false discovery rate correction was applied to reduce the risk of Type I error (FDR, Benjamini and Hochberg, 1995). Multiple regression and correlation analyses were done on Spatial Analysis in Macroecology (SAM v4.0).

3.3. Results

3.3.1. Physical data

Throughout the sampling period, wind speed was mostly >9m/s. During the period between April 2017 and May 2018, spatial variations in wind speed and direction were found at Skoenmakerskop and Chelsea Point, with wind speed values often exceeding 9 m/s (Figures 3.2 and 3.3). The prevalent direction changed between easterly (Figure 3.2A), westerlies (Figures 3.2B-E, G and 3.3F), southerlies (Figures 3.2F and 3.3A-E) and a northerly wind (Figure 3.3G). Since the study is focused on the easterly and westerly component, it was therefore concluded that the most dominant wind throught the sampling period was westerly. It is also noteworthy that during predominantly southerly winds, there were strong wind speeds (>9 m/s) coming from the east and west (Figures 3.3A-D; 3.4F; 3.5A, B, E, F; 3.6F; and 3.7A, B).

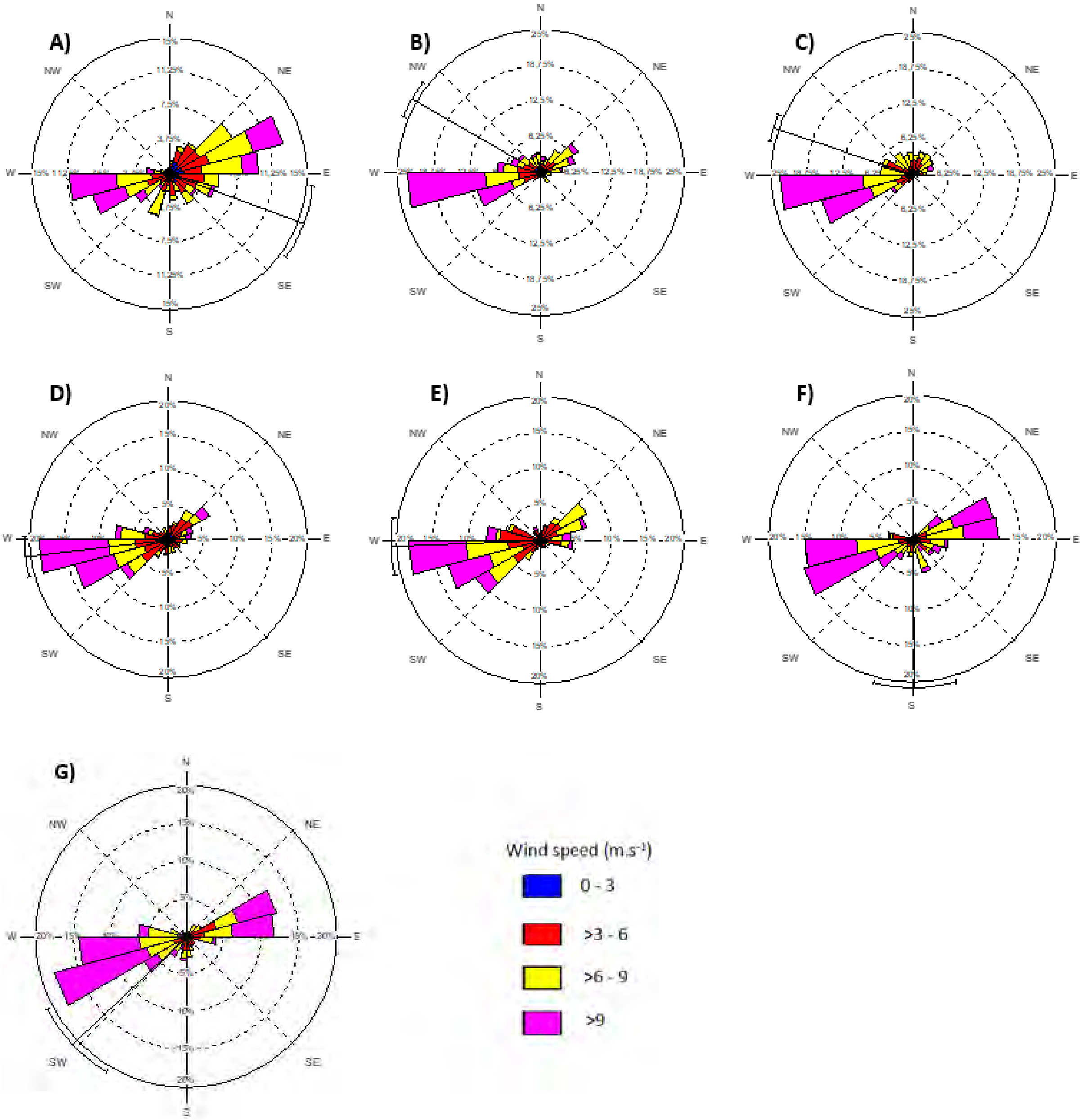

Figure 3.2 Wind data taken from a mid-point between Skoenmakerskop and Chelsea Point on **A)** 12 April–12 May 2017, **B)** 12 May–12 June 2017, **C)** 12 June–11 July 2017, **D)** 11 July–20 August 2017, **E)** 20 August–13 September 2017, **F)** 13 September–10 October 2017, **G)** 10 October–4 November 2017. The black vector and arc represent the mean direction and variability (standard deviation) from which the wind was coming from and the different colour sections indicate the frequency in percentages of a given wind speed from a given direction.

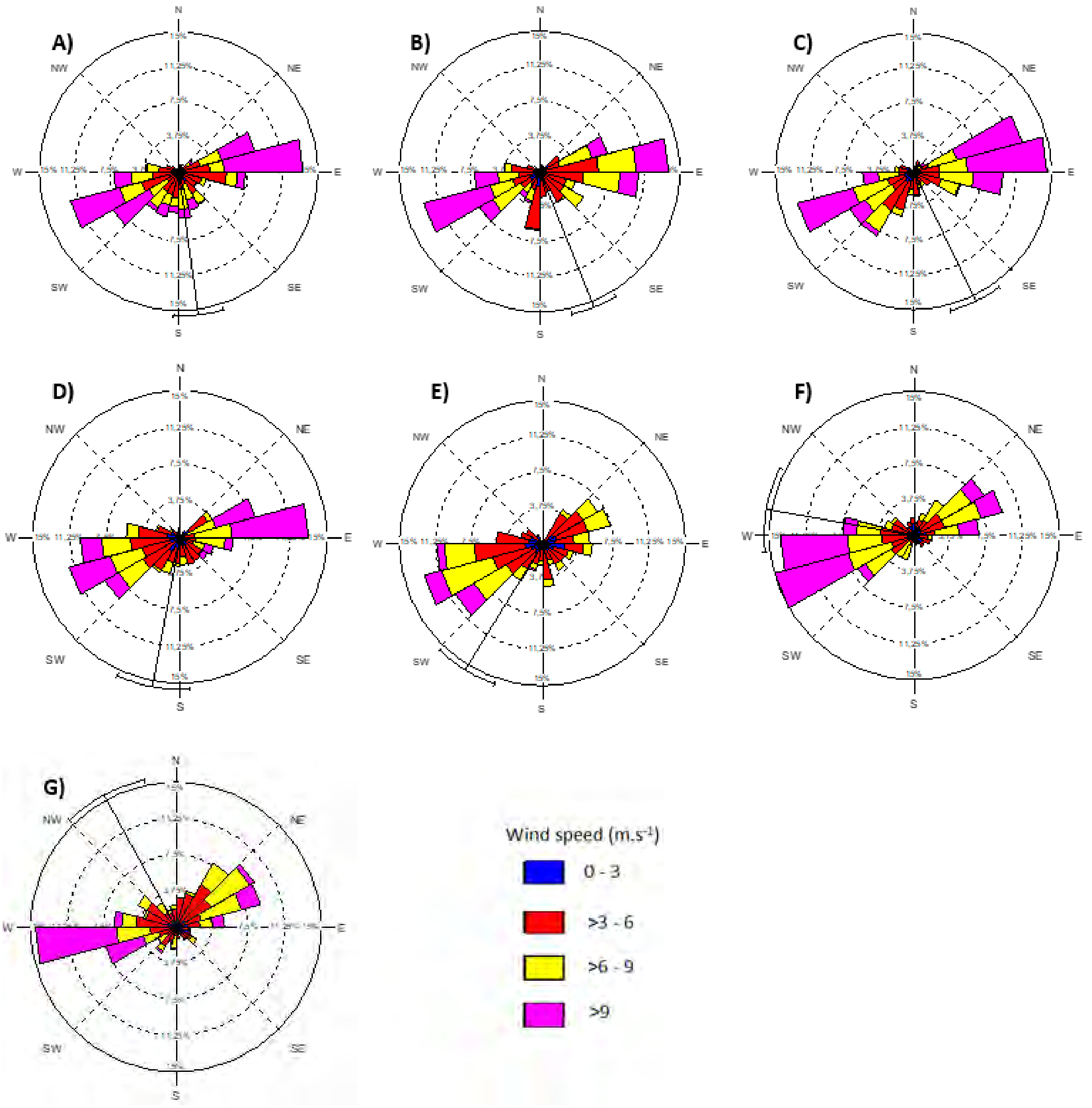

Figure 3.3: Wind data taken from a mid-point between Skoenmakerskop and Chelsea Point on **A)** 4 November–2 December 2017, **B)** 2 December 2017–4 January 2018, **C)** 4 January–2 February 2018, **D)** 2 February–4 March 2018, **E)** 4 March–5 April 2018, **F)** 5 April–1 May 2018, **G)** 1 May–31 May 2018. The black vector and arc represent the mean direction and variability (standard deviation) from which the wind was coming, and the different colour sections indicate the frequency in percentages of a given wind speed from a given direction.

From April 2017 to May 2018, there were spatial variations in wind speed and direction at Boardwalk and Brighton Beach, with wind speed values often exceeding 9 m/s (Figures 3.4 and 3.5). Easterlies (Figure 3.4A and 3.5C), westerlies (Figures 3.4B-E and 3.5F), southerlies (Figure 3.4F, G and 3.5A, B, D, E) and a northerly wind (Figure 3.5G) were present during this period. Overall though, westerly winds dominated during this period compared to easterlies.

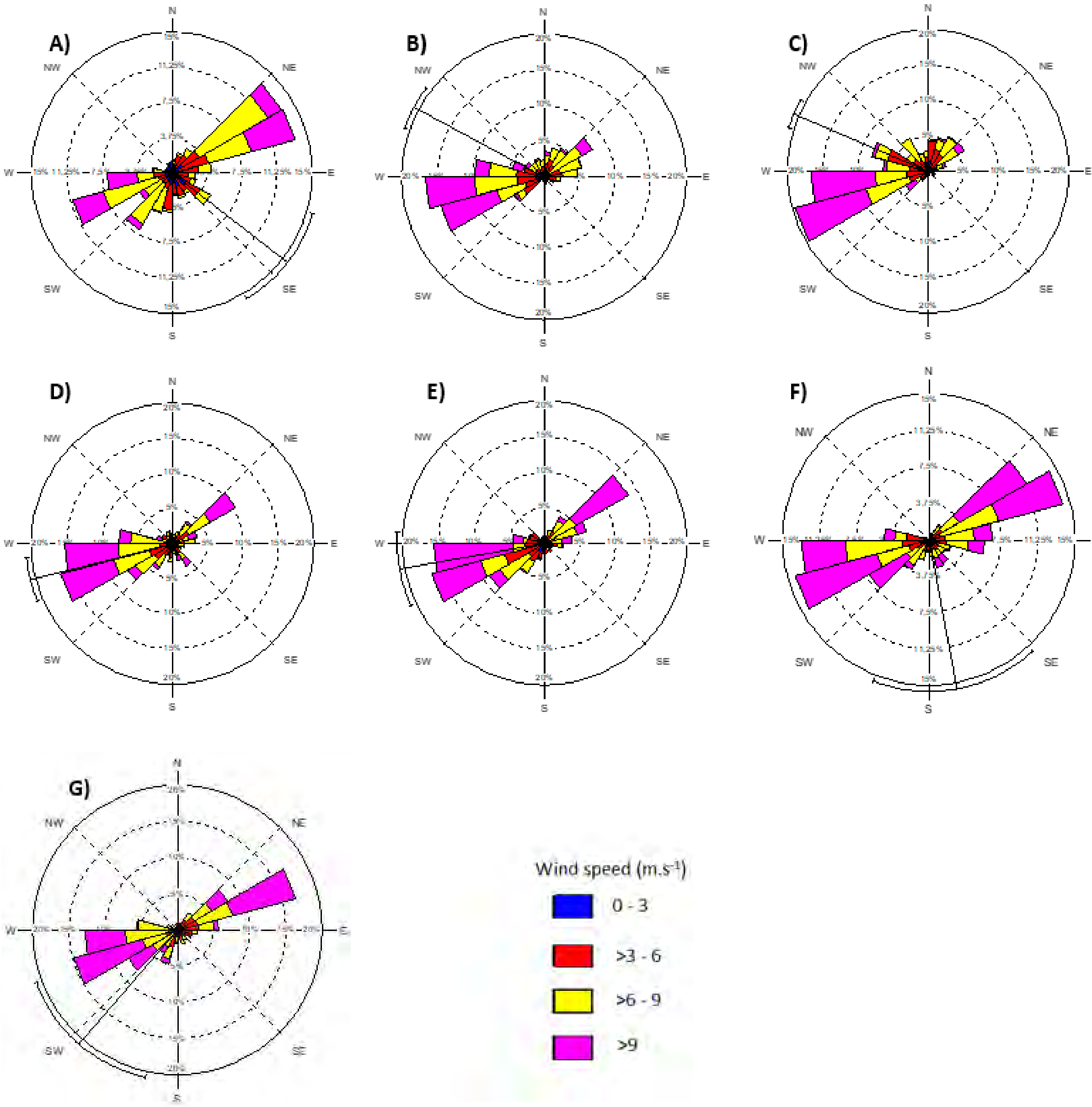

Figure 3.4: Wind data taken from a mid-point between Boardwalk and Brighton Beach on **A)** 11 April–11 May 2017, **B)** 11 May–13 June 2017, **C)** 13 June–12 July 2017, **D)** 12 July–19 August 2017, **E)** 19 August–12 September 2017, **F)** 12 September–11 October 2017, **G)** 11 October–5 November 2017. The black vector and arc represent the mean direction and variability (standard deviation) from which the wind was coming, and the different colour sections indicate the frequency in percentages of a given wind speed from a given direction.

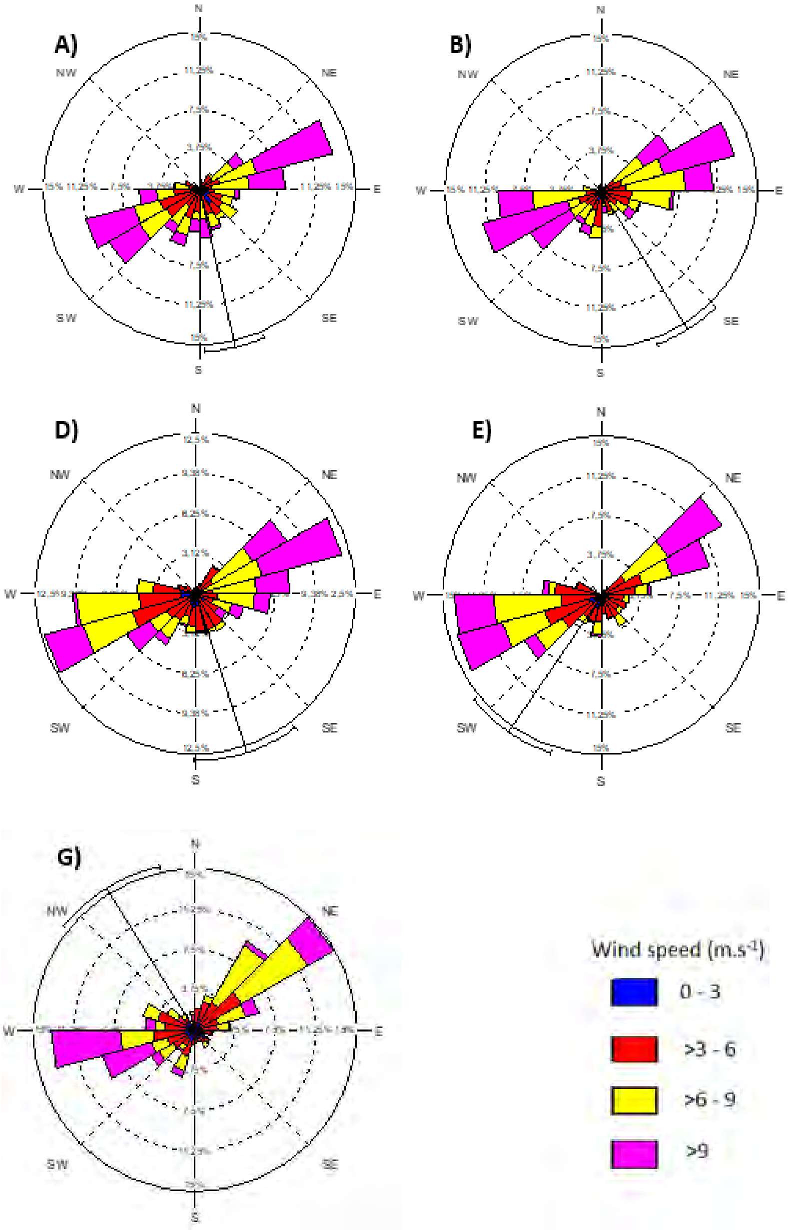

Figure 3.5: Wind data taken from a mid-point between Boardwalk and Brighton Beach on **A)** 4 November – 2 December 2017, **B)** 2 December 2017 – 4 January 2018, **C)** 4 January – 2 February 2018, **D)** 2 February – 4 March 2018, **E)** 4 March – 5 April 2018, **F)** 5 April – 1 May 2018, **G)** 1 May – 31 May 2018. The black vector and arc represent the mean direction and variability (standard deviation) wind was coming from and the different colour sections indicate the frequency in percentages of a given wind speed from a given direction.

Although wind speeds exceeded 9 m/s at Cannon Rocks and Kenton-on-Sea, they were not as prominent as the other four sites (Skoenmakerskop, Chelsea Point, Boardwalk, and Brighton Beach) (Figures 3.6 and 3.7). Another observation on these two sites is that there was no prevailing easterly wind present during the whole sampling period (April 2017 – May 2018). There were six months of predominant westerly winds (Figures 3.6B-F, G and 3.7F), two months of predominantly northerly winds (Figure and 3.7G) and six months of southerly winds (Figures 3.6F and 3.7A-E).

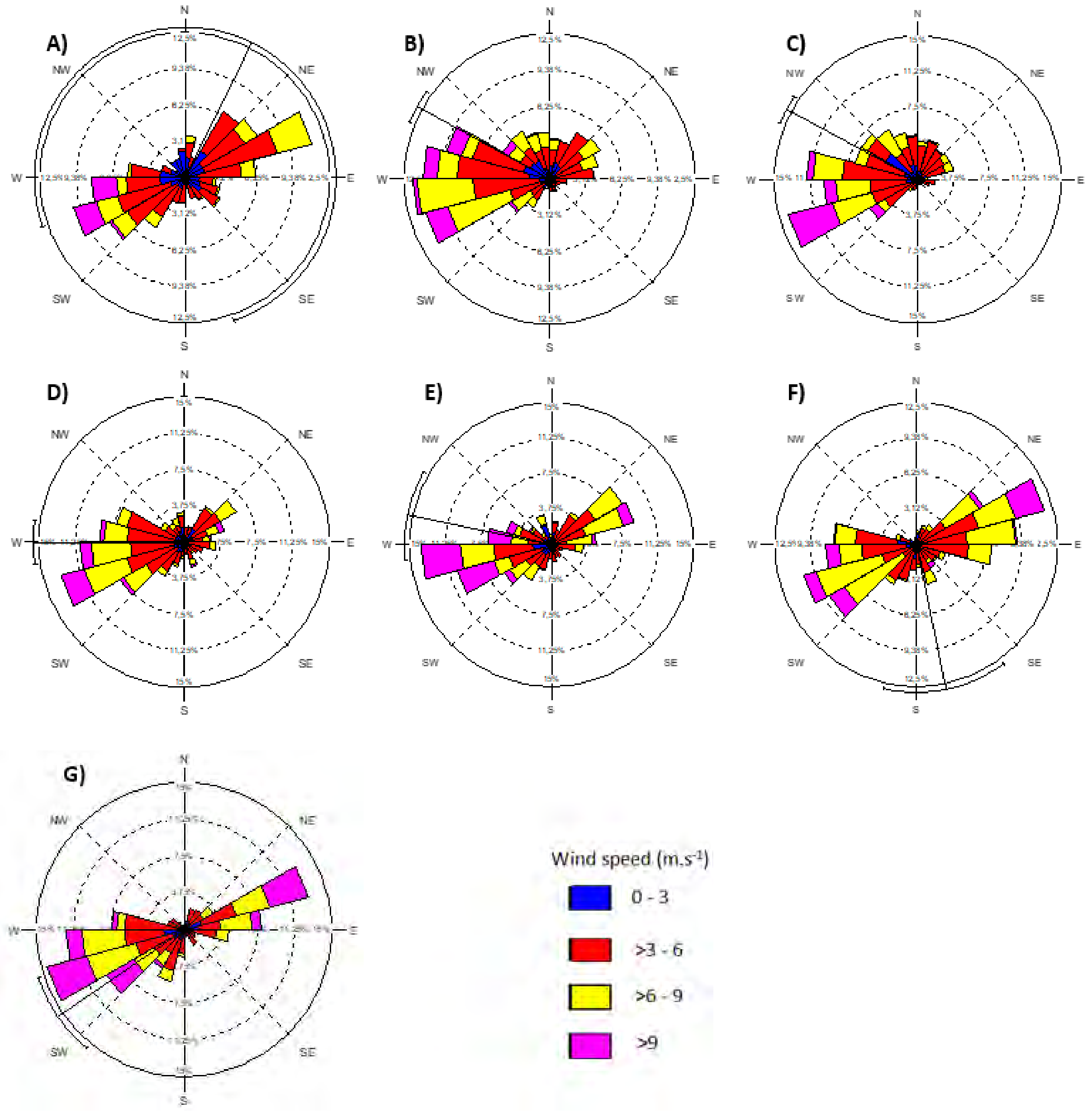

Figure 3.6: Wind data taken from a mid-point between Cannon Rocks and Kenton-On-Sea on **A)** 11 April – 11 May 2017, **B)** 11 May – 13 June 2017, **C)** 13 June – 12 July 2017, **D)** 12 July – 19 August 2017, **E)** 19 August – 12 September 2017, **F)** 12 September – 11 October 2017, **G)** 11 October – 5 November 2017. The black vector and arc represent the mean direction and variability (standard deviation) wind was coming from and the different colour sections indicate the frequency in percentages of a given wind speed from a given direction.

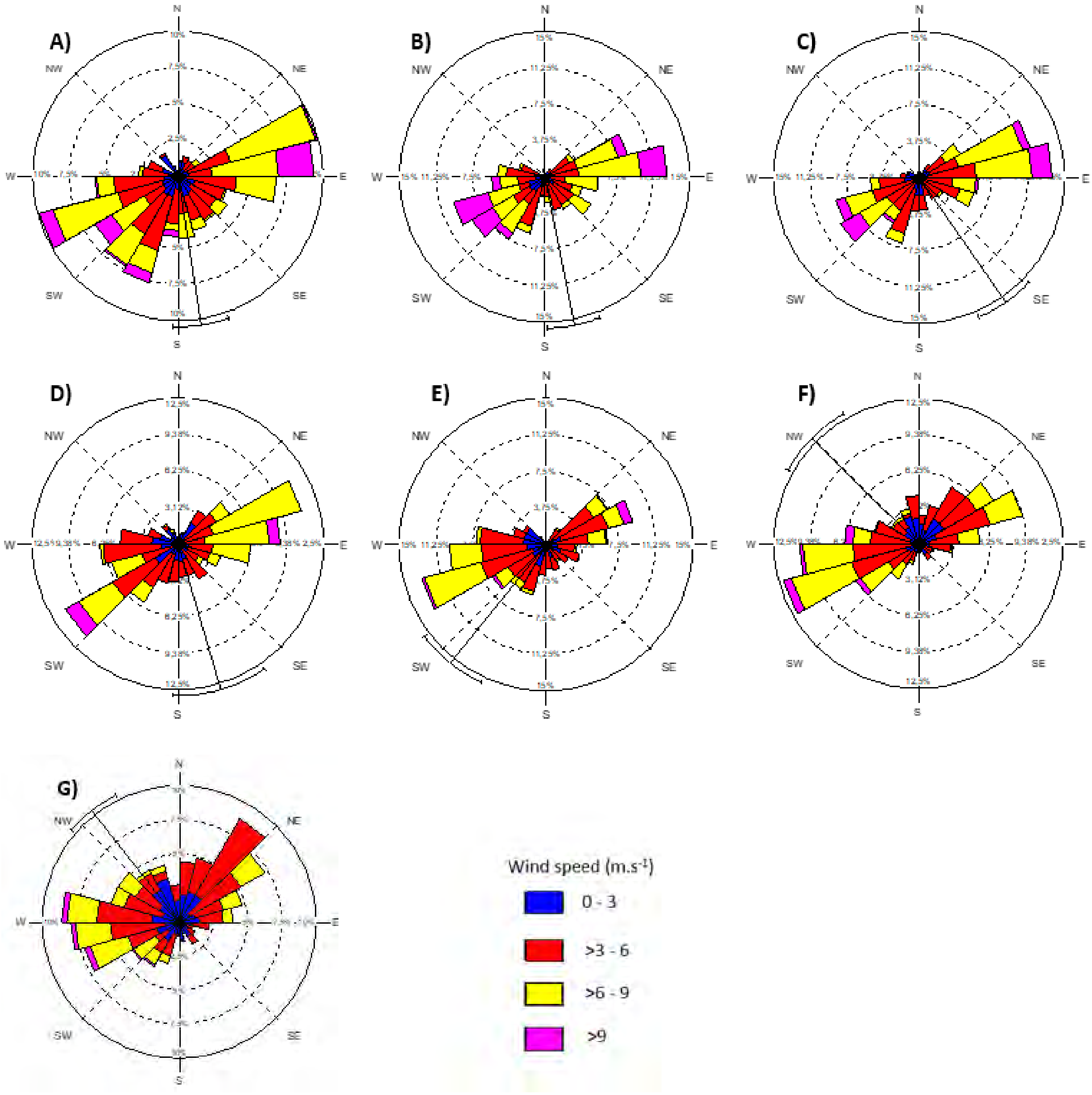

Figure 3.7: Wind data taken from a mid-point between Cannon Rocks and Kenton-On-Sea on **A)** 5 November – 3 December 2017, **B)** 3 December 2017 – 5 January 2018, **C)** 5 January – 1 February 2018, **D)** 1 February – 3 March 2018, **E)** 3 March – 3 April 2018, **F)** 3 April – 2 May 2018, **G)** 2 May – 30 May 2018. The black vector and arc represent the mean direction and variability (standard deviation) wind was coming from and the different colour sections indicate the frequency in percentages of a given wind speed from a given direction.

3.1.1. Biological data

With the Benjamini-Hochberg correction, the alpha value was still 0.05 (Appendix: Table A3) as all the individual factors and the interaction were significant, at $p < 0.0001$ (Tables 3.1–3.8). For all analyses exploring the effects of month and site on the abundances of different taxa, the interaction of month and site was significant, for each of the taxa investigated (Tables 3.1–3.8), indicating that sites behaved differently in respect to the timing of settlement and recruitment. The post-hoc grouping results revealed variations in taxon abundances among different sites within the same month (Figures 3.6A–3.13A).

Perna perna settlers

Although monthly site variability was noted throughout the sampling period (Figure 3.6A), the overall abundance of *P. perna* settlers was highest in June 2018 and lowest in January 2018 (Figure 3.6B). At peak settler abundance, in June 2018, the sites within the bay (BDW and BB) had statistically higher abundances than sites outside the bay (SK, CP, CR, and KOS). The same trend was noted in February and May 2018. When settler abundances were lowest, in January 2018 (Figure 3.6B), there were no significant differences among sites (Figure 3.6A).

Table 3.1: ANOVA examining the effects of Month and Site on the abundance [$\log_{10}(x+1)$] of *Perna perna* settlers at six different sites over 14 sampling months. SS – Sum of Squares; df – degrees of freedom; MS – Mean Squares; F – F-ratios; and p – p-values (significant values in bold).

Effect	SS	Df	MS	F	P
Month	32.511	13	2.501	33.279	**<0.0001**
Site	6.568	5	1.314	17.480	**<0.0001**
Month*Site	15.905	65	0.245	3.256	**<0.0001**
Error	12.625	168	0.075		

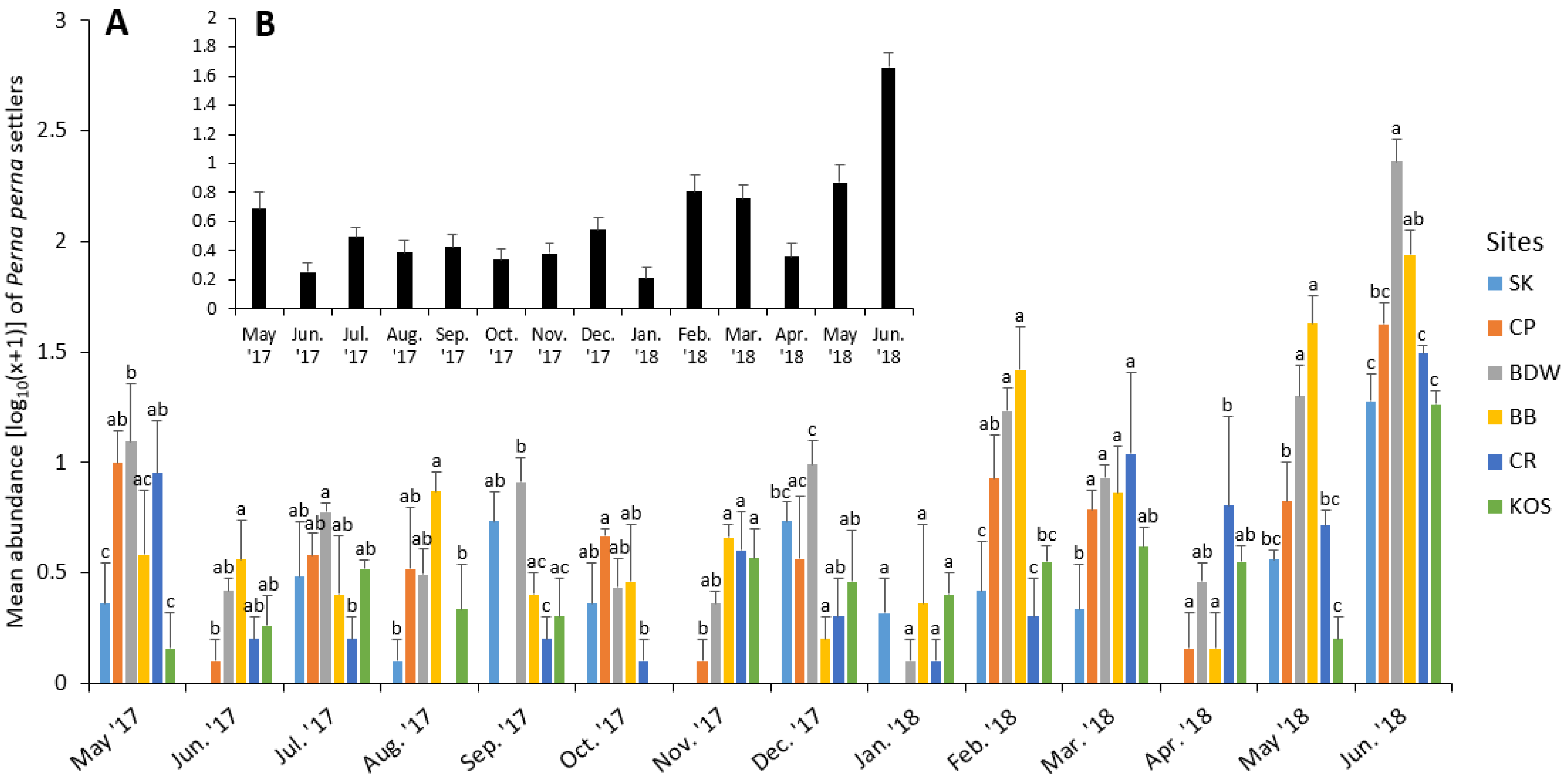

Figure 3.6: **A**) Mean abundance [$\log_{10}(x+1)$] of *Perna perna* settlers at six sites over a 14-month sampling period. Letters above the histogram bars indicate homogenous groups identified by a post-hoc test performed on the effect of site within each month. **B**) Inset graph with black bars shows average abundance of *P. perna* settlers per month, across all sites. Error bars indicate standard errors. Site abbreviations are as in Table 3.1. Note that zero values indicate that no settlers were found at those sites during the given months.

Perna perna recruits

There was a decline in the abundance of *P. perna* recruits from May to September 2017, which then increased to a peak between February and April 2018, and thereafter declined until the end of the sampling period in June 2018 (Figure 3.7B). As was found in the earlier settler stage, recruits were found in higher abundances within the bay than on the open coast (Figure 3.7A). In five months (October, November, and December 2017, February and March 2018), the highest recruit abundances were recorded at the sites within the bay (BDW and BB), with generally lower values at the open coast sites of SK, CP, CR, and KOS (Figure 3.7A). In June 2018, BDW showed the highest peak in recruit abundance.

Table 3.2: ANOVA examining the effects of Month and Site on *P*. *perna* recruits [$\log_{10}(x+1)$] settling at six different sites over 14 sampling months. SS – Sum of Squares; df – degrees of freedom; MS – Mean Squares; F – F-ratios; and p – p-values (significant values in bold).

Effect	SS	df	MS	F	P
Month	55.108	13	4.239	66.478	**<0.0001**
Site	18.049	5	3.610	56.608	**<0.0001**
Month*Site	27.799	65	0.428	6.707	**<0.0001**
Error	10.713	168	0.064		

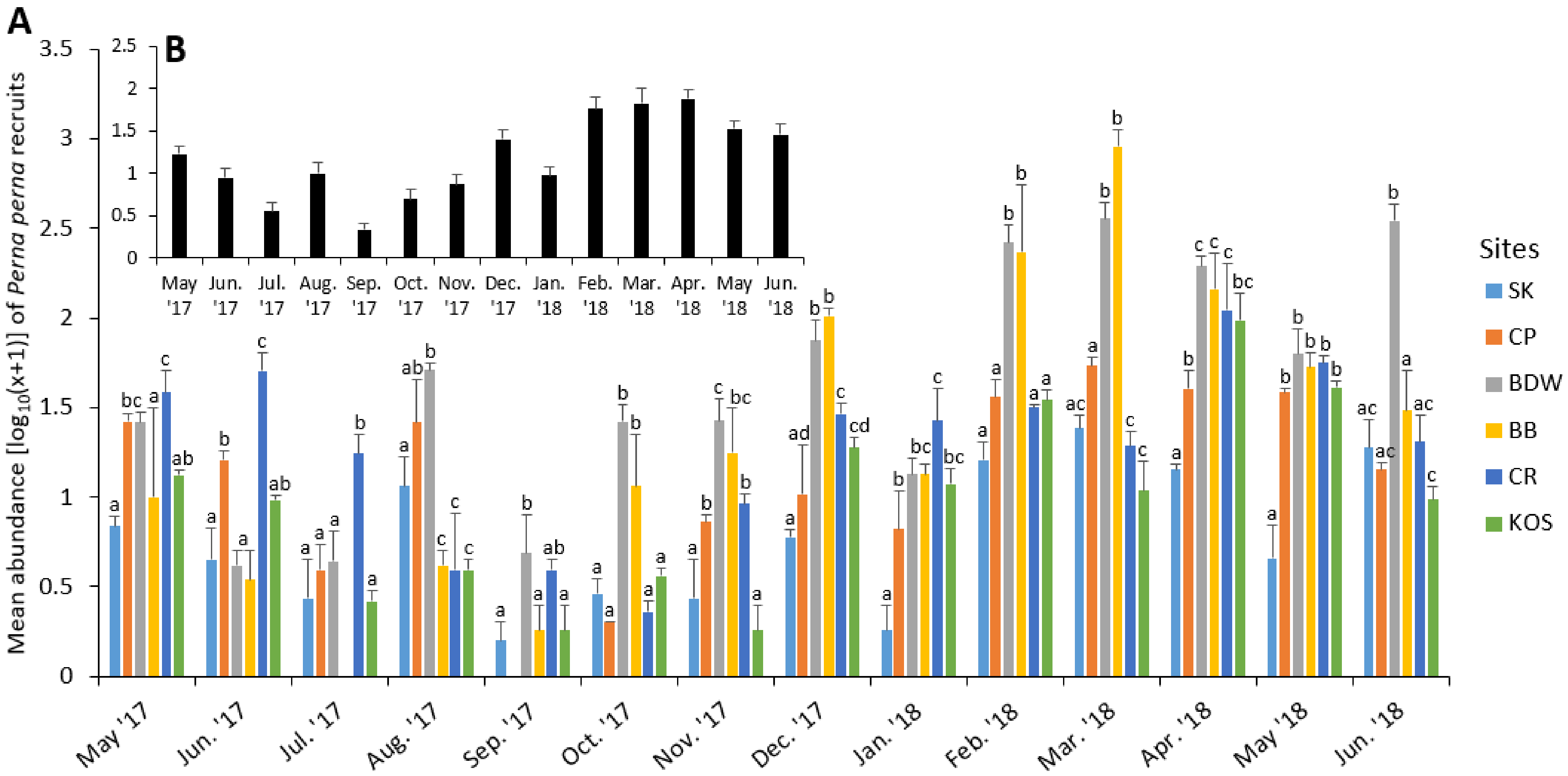

Figure 3.7: **A**) Mean abundance [$\log_{10}(x+1)$] of *Perna perna* recruits at six sites over a 14-month sampling period. Letters above the histogram bars indicate homogenous groups identified by a post-hoc test performed on the effect of site within each month. **B**) Inset graph with black bars shows average abundance of *P. perna* recruits per month, across all sites. Error bars indicate standard errors. Site abbreviations are as in Table 3.1. Note that zero values indicate that no recruits were found at those sites during the given months.

Mytilus galloprovincialis settlers

M. galloprovincialis settler abundances were high in October and December 2017, and in February and June 2018 (Figure 3.8B). In December 2017, the three western sites of SK, CP and BDW had similar abundances, which were statistically higher than those at the three eastern sites of BB, CR and KOS (Figure 3.8A). In February 2018, BDW and CP had similar abundances, which were statistically higher than the other sites. Abundances at BDW were statistically higher than at BB in June 2018, followed by all the other sites which presented similar abundances (Figure 3.8A).

Table 3.3: ANOVA examining the effects of Month and Site on the settlement [$\log_{10}(x+1)$] of *Mytilus galloprovincialis* settlers at six different sites over 14 sampling months. SS – Sum of Squares; df – degrees of freedom; MS – Mean Squares; F – F-ratios; and p – p-values (significant values in bold).

Effect	SS	df	MS	F	p
Month	41.342	13	3.180	39.704	**<0.0001**
Site	11.835	5	2.367	29.553	**<0.0001**
Month*Site	25.479	65	0.392	4.894	**<0.0001**
Error	13.456	168	0.080		

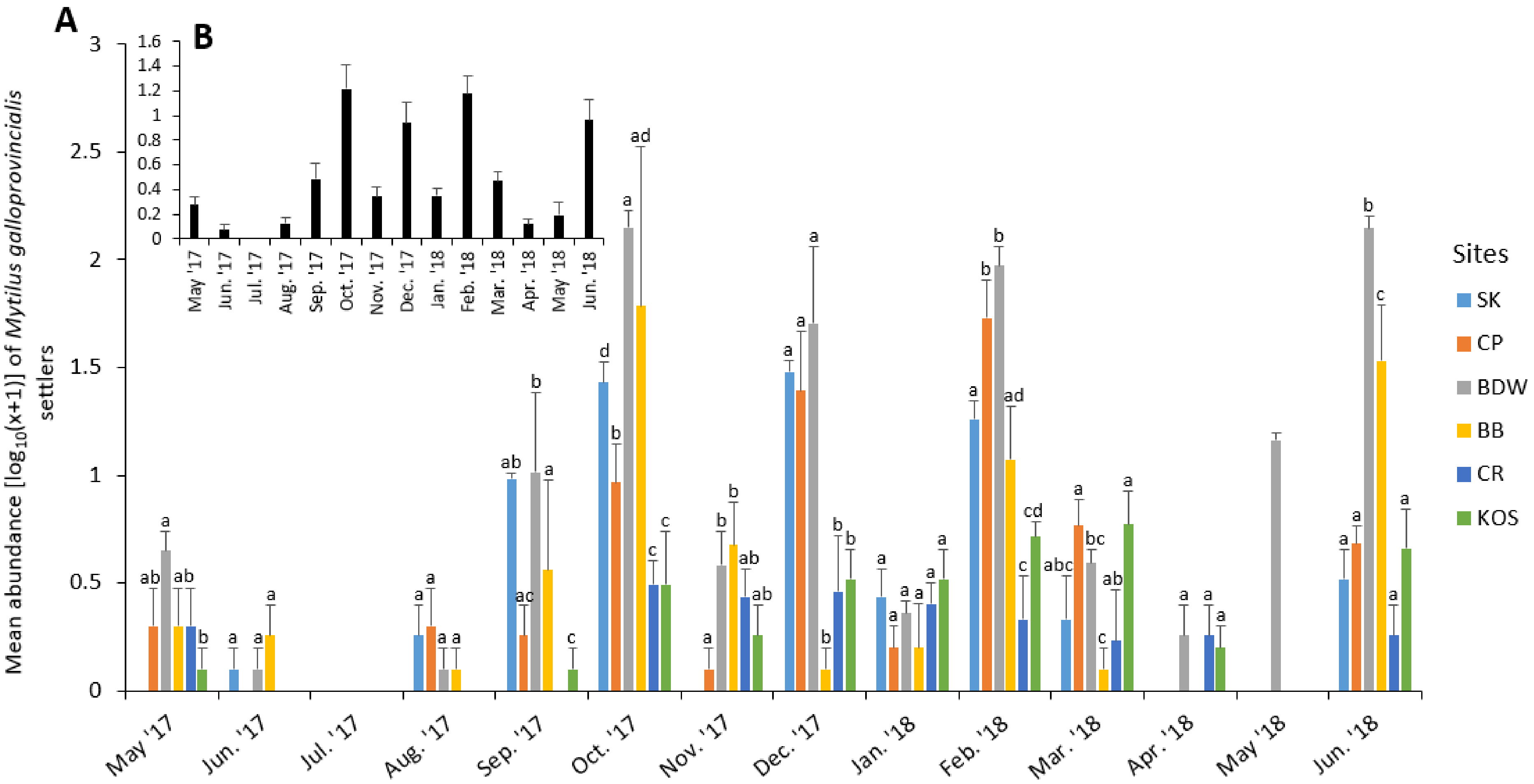

Figure 3.8: **A**) Mean abundance [$\log_{10}(x+1)$] of *Mytilus galloprovincialis* settlers at six sites over a 14-month sampling period. Letters above the histogram bars indicate homogenous groups identified by a post-hoc test performed on the effect of site within each month. **B**) Inset graph with black bars shows average abundance of *M. galloprovincialis* settlers per month, across all sites. Error bars indicate standard errors. Site abbreviations are as in Table 3.1. Note that zero values indicate that no settlers were found at those sites during the given months.

Mytilus galloprovincialis recruits

As observed for *P. perna* recruits, but with more pronounced differences, the abundance of *M. galloprovincialis* recruits showed an increase to a peak month, then a decline towards the end of the study period (Figure 3.9B). Similar to *P. perna*, the peak was recorded in February 2018. For six out of the 14 months of sampling (May and August 2017, January, February, April and June 2018), BDW had statistically higher abundances than the other sites (Figure 3.9A). Additionally, over four months (September, October, November and December 2017), the bay sites of BDW and BB had higher abundances than the open coast sites of SK, CP, CR and KOS. The lowest abundances were recorded in July 2017 (Figure 3.9B), when abundance of recruits was similar across sites (Figure 3.9A).

Table 3.4: ANOVA examining the effects of Month and Site on *M. galloprovincialis* recruits [$\log_{10}(x+1)$] settling at six different sites over 14 sampling months. SS – Sum of Squares; df – degrees of freedom; MS – Mean Squares; F – F-ratios; and p – p-values (significant values in bold).

Effect	SS	Df	MS	F	p
Month	47.044	13	3.619	53.106	**<0.0001**
Site	17.160	5	3.432	50.364	**<0.0001**
Month*Site	17.385	65	0.268	3.925	**<0.0001**
Error	11.448	168	0.068		

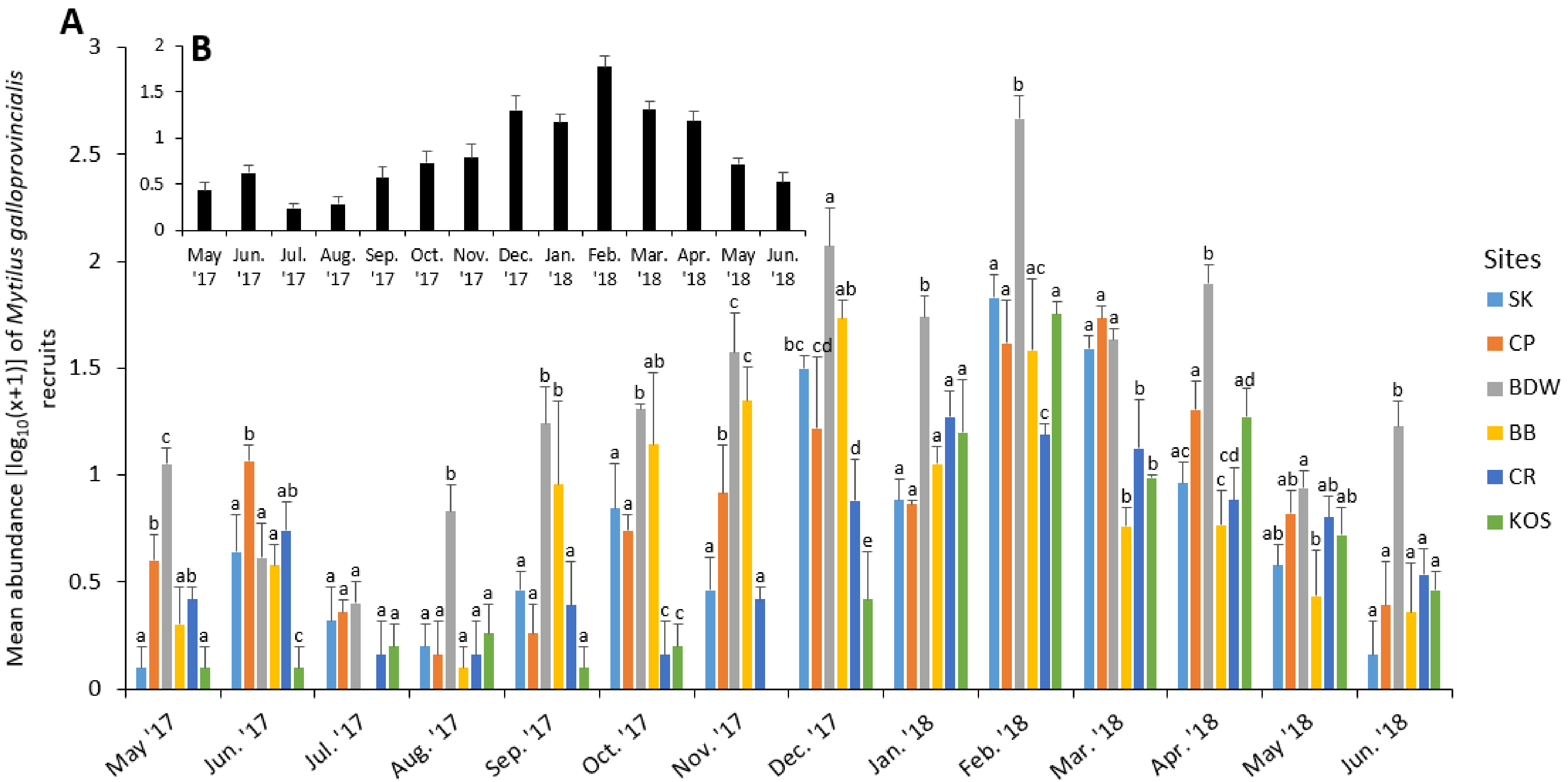

Figure 3.9: **A**) Mean abundance [$\log_{10}(x+1)$] of *Mytilus galloprovincialis* recruits at six sites over a 14-month sampling period. Letters above the histogram bars indicate homogenous groups identified by a post-hoc test performed on the effect of site within each month. **B**) Inset graph with black bars shows average abundance of *M. galloprovincialis* recruits per month, across all sites. Error bars indicate standard errors. Site abbreviations are as in Table 3.1. Note that zero values indicate that no recruits were found at those sites during the given months.

Total settlers (*P*. *perna* and *M*. *galloprovincialis* combined)

The peak months for total settler abundances were October and December 2017, and February and June 2018 (Figure 3.10B). In October 2017, May and June 2018, abundances were higher at the bay (BDW and BB) than the open coasts sites (SK, CP, CR, and KOS) (Figure 3.10A). In December 2017, the western sites (SK, CP, and BDW) had statistically higher abundances than the western sites of BB, CR, and KOS.

Table 3.5: ANOVA examining the effects of Month and Site on the abundance [$\log_{10}(x+1)$] of total settlers settling at six different sites over 14 sampling months. SS – Sum of Squares; df – degrees of freedom; MS – Mean Squares; F – F-ratios; and p – p-values (significant values in bold).

Effect	SS	df	MS	F	p
Month	42.416	13	3.263	30.938	**<0.0001**
Site	12.127	5	2.425	22.997	**<0.0001**
Month*Site	26.670	65	0.410	3.891	**<0.0001**
Error	17.718	168	0.106		

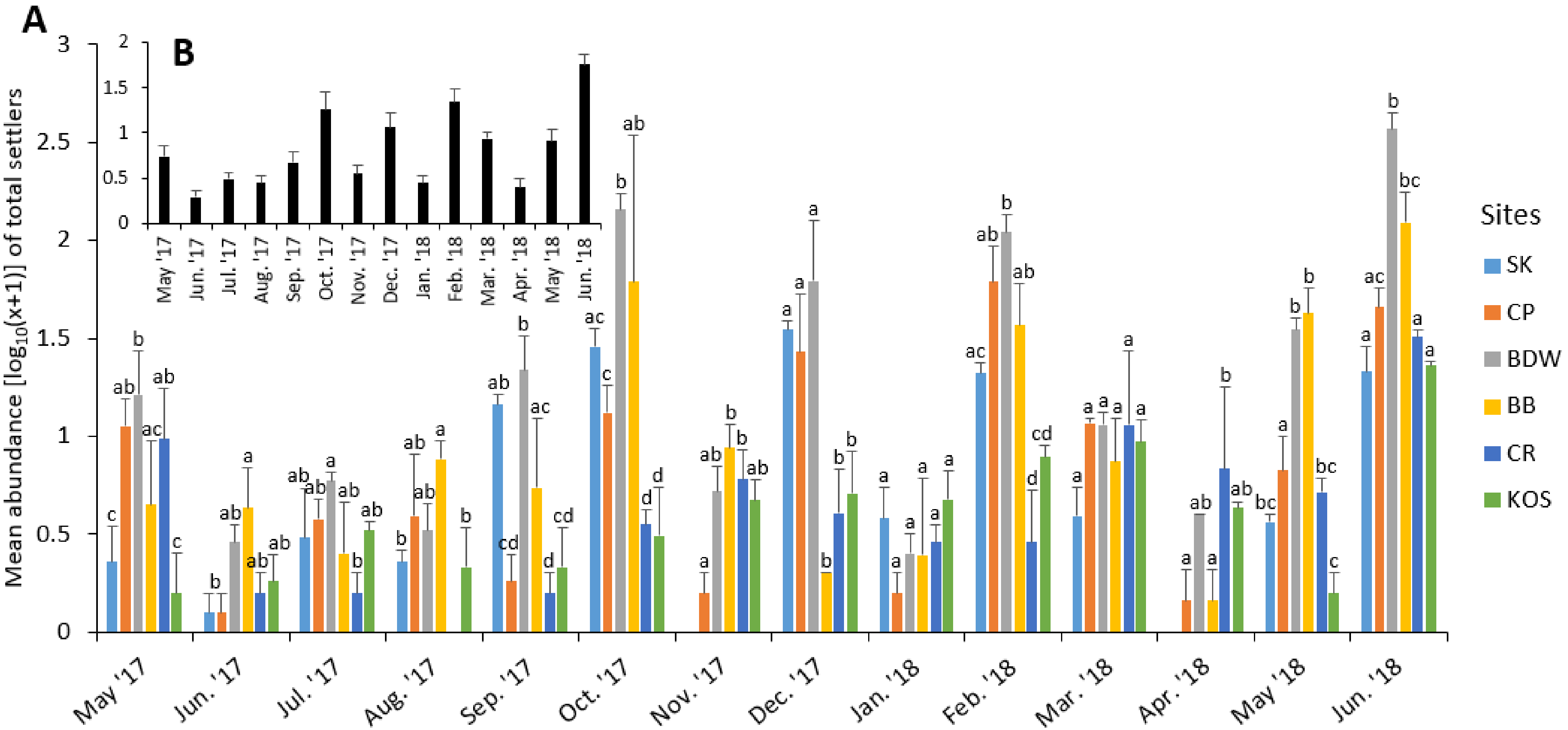

Figure 3.10: **A**) Mean abundance [$\log_{10}(x+1)$] of total mussel settlers at six sites over a 14-month sampling period. Letters above the histogram bars indicate homogenous groups identified by a post-hoc test performed on the effect of site within each month. **B**) Inset graph with black bars shows average abundance of total mussel settlers per month, across all sites. Error bars indicate standard errors. Site abbreviations are as in Table 3.1. Note that zero values indicate that no settlers were found at those sites during the given months.

Total recruits (*P. perna* and *M. galloprovincialis* combined)

Recruit abundances showed a seasonal pattern, with low numbers at the end of winter and spring (July to November 2017, except August 2017), rising to a peak in late summer (February 2018) and slowly decreasing towards winter (June 2018) (Figure 3.11B). During the rise in abundance from late spring, October 2017 to the peak in February–March 2018, the bay sites of BDW and BB had significantly higher abundances in four (October and December 2017, and February and March 2018) of these six months, with the exception of November 2017, when BB was not significantly different to CP, and January 2018, when BDW shared similarities with CR and KOS, and BB shared a similarity with CP (Figure 3.11A).

Table 3.6: ANOVA examining the effects of Month and Site on the abundance [$\log_{10}(x+1)$] of total recruits settling at six different sites over 14 sampling months. SS – Sum of Squares; df – degrees of freedom; MS – Mean Squares; F – F-ratios; and p – p-values (significant values in bold).

Effect	SS	df	MS	F	p
Month	52.986	13	4.076	60.601	**<0.0001**
Site	17.332	5	3.467	51.541	**<0.0001**
Month*Site	24.214	65	0.373	5.539	**<0.0001**
Error	11.299	168	0.067		

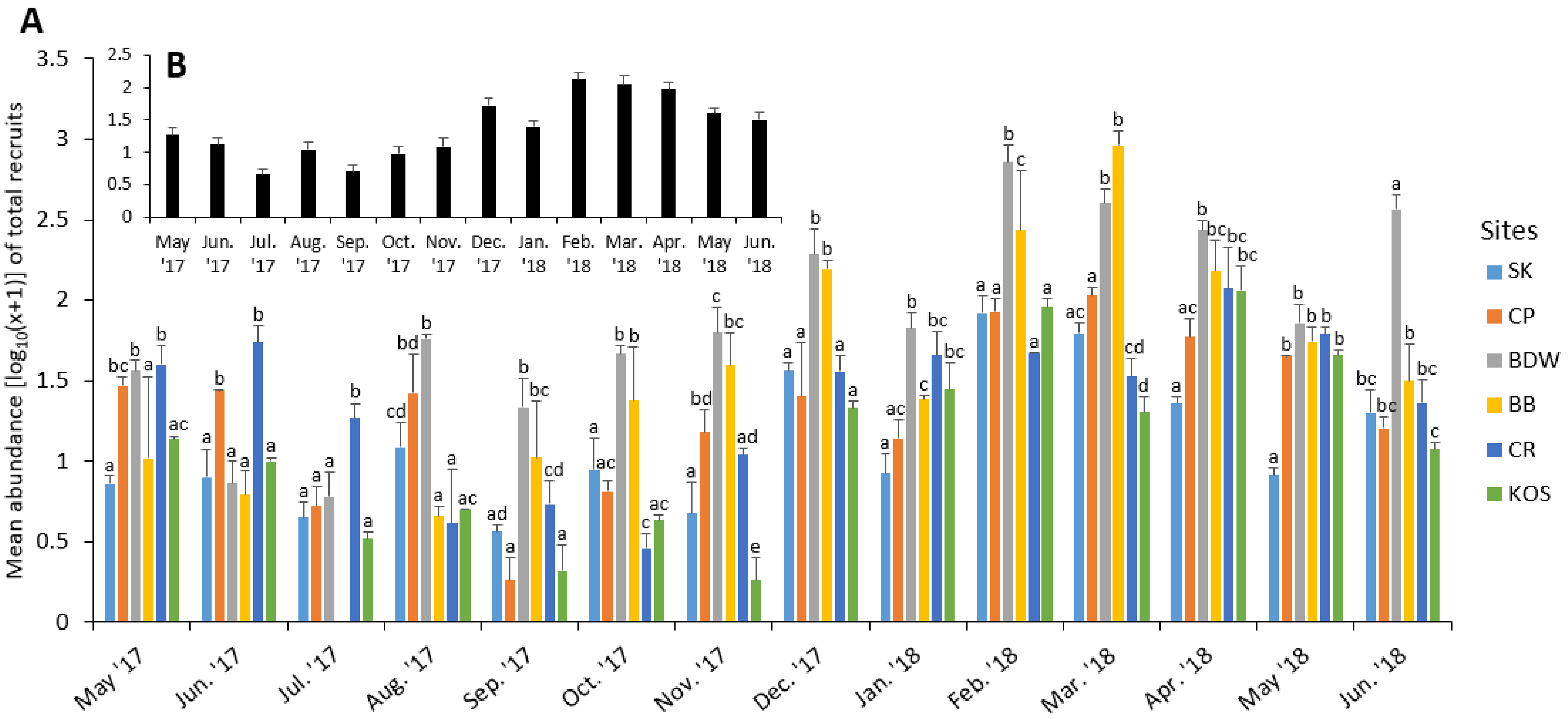

Figure 3.11: **A**) Mean abundance [$\log_{10}(x+1)$] of total mussel recruits at six sites over a 14-month sampling period. Letters above the histogram bars indicate homogenous groups identified by a post-hoc test performed on the effect of site within each month. **B**) Inset graph with black bars shows average abundance of unidentified bivalves per month, across all sites. Error bars indicate standard errors. Site abbreviations are as in Table 3.1. Note that zero values indicate that no recruits were found at those sites during the given months.

Barnacle cyprids

Out of 14 months, there were no records of barnacle cyprids at any of the sites during three months (August and September 2017, and June 2018; Figure 3.12B), with abundances (per 100 cm^2) recorded only at BDW in another three months (July, October, and November 2017; Figure 3.12A). Cyprids were recorded at more than one site in eight months (May, June and December 2017, January, February, March, April, and May 2018), and for six of these months (May and June 2017, January, March, April, and May 2018), BDW had significantly higher abundances than all the other sites (Figure 3.12A). Thus, cyprids were either recorded only at BDW, or at abundances that were almost always significantly higher at BDW.

Table 3.7: ANOVA examining the effects of Month and Site on the abundance [$\log_{10}(x+1)$] of barnacle cyprids settling at six different sites over 14 sampling months. SS – Sum of Squares; df – degrees of freedom; MS – Mean Squares; F – F-ratios; and p – p-values (significant values in bold).

Effect	SS	df	MS	F	p
Month	7.709	13	0.593	20.995	**<0.0001**
Site	14.837	5	2.967	105.059	**<0.0001**
Month*Site	22.407	65	0.345	12.205	**<0.0001**
Error	21.353	756	0.028		

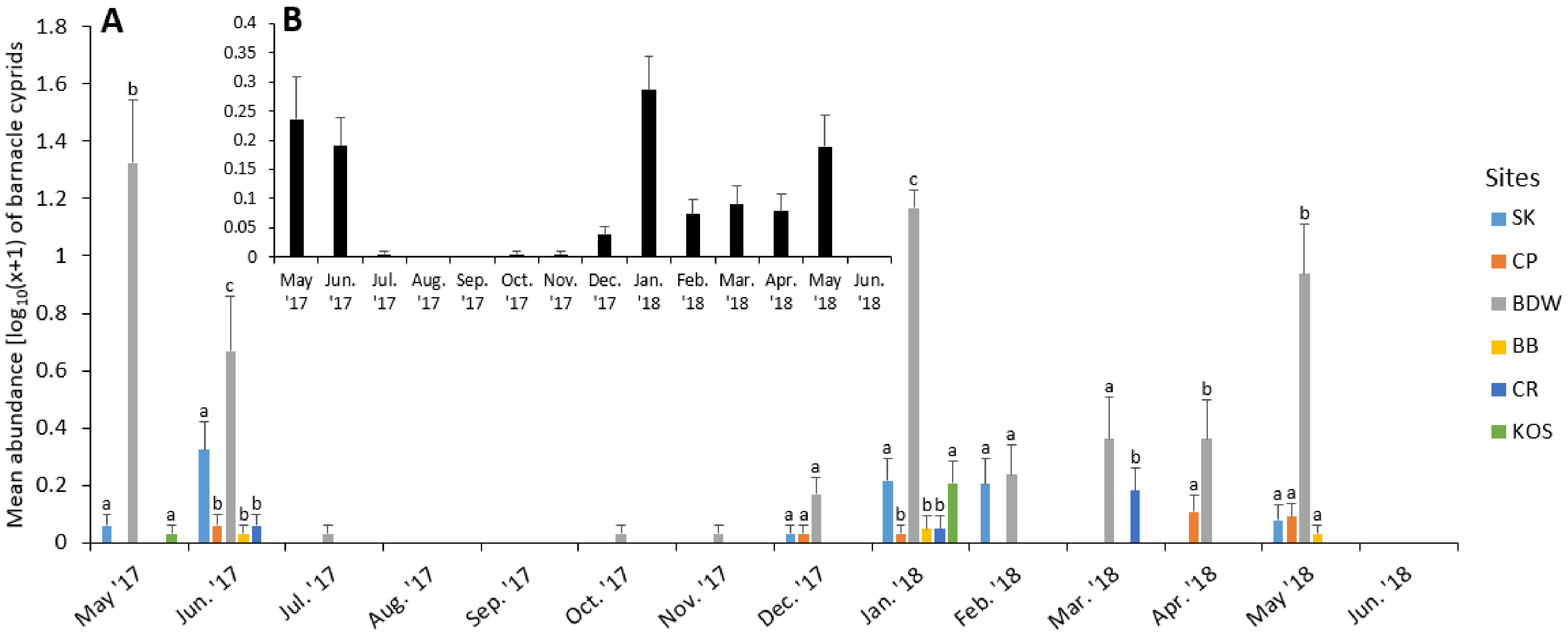

Figure 3.12: **A**) Mean abundance [$\log_{10}(x+1)$] of barnacle cyprids at six sites over a 14-month sampling period. Letters above the histogram bars indicate homogenous groups identified by a post-hoc test performed on the effect of site within each month. **B**) Inset graph with black bars shows average abundance of barnacle cyprids per month, across all sites. Error bars indicate standard errors. Site abbreviations are as in Table 3.1. Note that zero values indicate that no cyprids were found at those sites during the given months.

Juvenile barnacles

High abundances were recorded in May, June, and July 2017, with peak values in February 2018 (Figure 3.13B). In May 2017, BDW had the statistically highest abundance, whilst in June 2017, SK and BDW shared similar abundances (Figure 3.13A). In July 2017 and February 2018, statistically higher abundances were recorded at SK (Figure 3.13A).

Table 3.8: ANOVA examining the effects of Month and Site on the abundance [$\log_{10}(x+1)$] of juvenile barnacles at six different sites over 14 sampling months. SS – Sum of Squares; df – degrees of freedom; MS – Mean Squares; F – F-ratios; and p – p-values (significant values in bold).

Effect	SS	df	MS	F	p
Month	52.174	13	4.013	54.538	**<0.0001**
Site	18.597	5	3.719	50.544	**<0.0001**
Month*Site	35.087	65	0.540	7.335	**<0.0001**
Error	55.632	756	0.074		

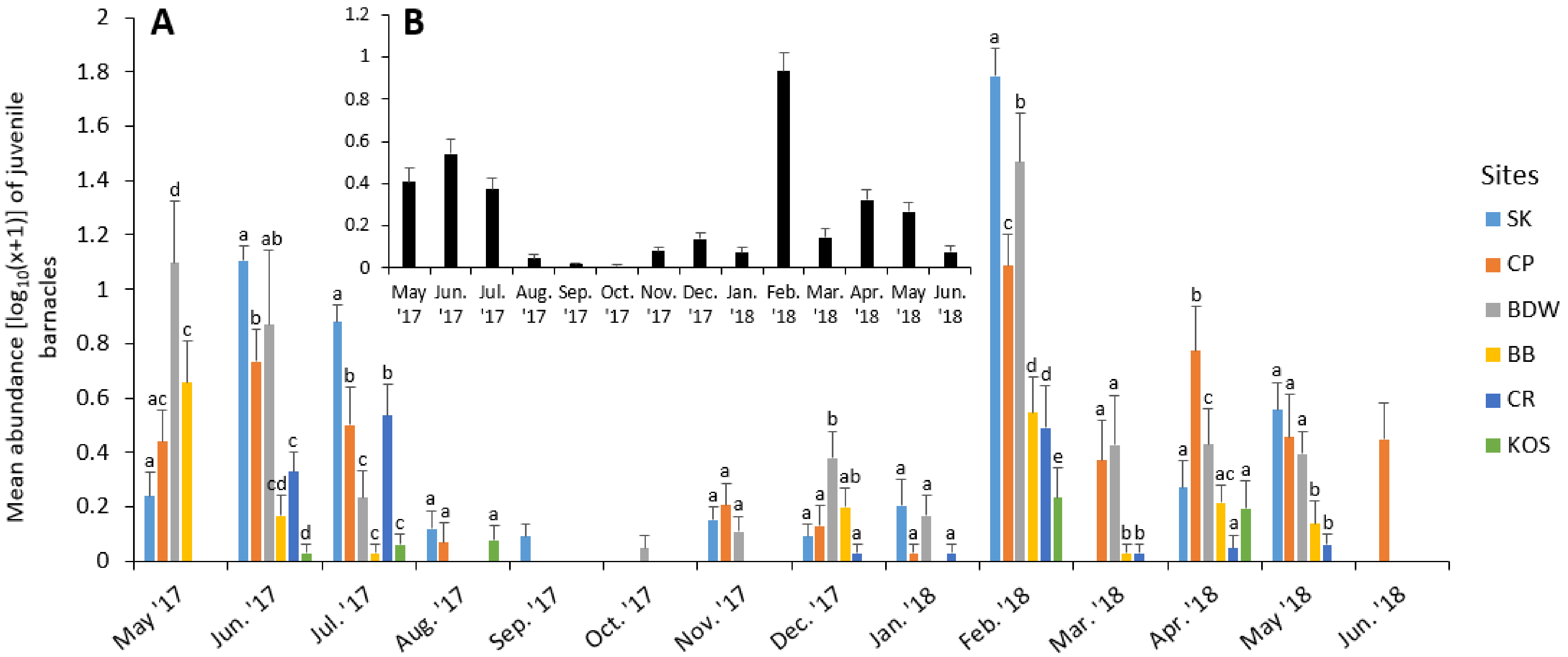

Figure 3.13: **A**) Mean abundance [$\log_{10}(x+1)$] of juvenile barnacles at six sites over a 14-month sampling period. Letters above the histogram bars indicate homogenous groups identified by a post-hoc test performed on the effect of site within each month. **B**) Inset graph with black bars shows average abundance of juvenile barnacles per month, across all sites. Error bars indicate standard errors. Site abbreviations are as in Table 3.1. Note that zero values indicate that no juvenile barnacles were found at those sites during the given months.

3.1.2. Bio-physical relationships

Multiple linear regression analyses

Possible relationships between the physical variables of upwelling and the dissipation of turbulent kinetic energy and the mussel settler and recruit, barnacle cyprid and juvenile larval abundances at different sites were investigated using multiple linear regression analyses. Shorter time lags (12 hours, 24 hours, and 2 days) were used to assess relationships with mussel settlers and barnacle cyprids, while longer time lags (24 hours, 2 days, 4 days, 7 days, 14 days, and 1 month) were considered for mussel recruitment and barnacle juveniles. With multiple tests being performed, the likelihood of having a Type I error was high and this was mitigated by the application of the Benjamini-Hochberg correction, which resulted in a new alpha value of 0.001 (Appendix: Table A4).

Both, the upwelling index and the dissipation of turbulent kinetic energy had no significant relationship with *Perna perna*, *Mytilus galloprovincialis* and the combination of both species' settler (total settlers) abundances at all the sites (Table 3.9).

Table 3.9: Multiple linear regression analysis showing the relationship between physical variables and settlers of each taxon at a given site over different time lags. For each relationship, +/- is the sign of the regression, p-value is the level of significance, R^2 is total variation explained and AIC indicates the Akaike Information Criterion. Significant results ($p < 0.001$) are shown in bold. SK = Skoenmakerskop, CP = Chelsea Point, BDW = Boardwalk, BB = Brighton Beach, CR = Cannon Rocks and KOS = Kenton-on-Sea.

Site	Variable	Lag	*Perna perna* settlers				*Mytilus galloprovincialis* settlers				Total settlers			
			Sign	p-value	R^2	AIC	Sign	p-value	R^2	AIC	Sign	p-value	R^2	AIC
SK	Upwelling	12 hours	+	0.546	0.034	10.481	+	0.857	0.003	30.702	+	0.712	0.013	28.201
		24 hours	+	0.943	0.001	10.927	+	0.527	0.037	30.247	+	0.634	0.021	28.089
		2 days	+	0.992	0.001	10.933	+	0.102	0.224	27.443	+	0.338	0.084	27.236
	Dissipation of turbulent kinetic energy	12 hours	+	0.489	0.045	10.341	+	0.652	0.019	30.49	+	0.571	0.03	27.972
		24 hours	+	0.378	0.071	9.971	+	0.533	0.036	30.261	+	0.426	0.058	27.587
		2 days	+	0.914	0.001	10.918	+	0.337	0.084	29.603	+	0.505	0.041	27.821
CP	Upwelling	12 hours	+	0.961	0.001	19.507	+	0.698	0.014	31.294	+	0.867	0.003	29.361
		24 hours	+	0.761	0.009	19.395	+	0.731	0.011	31.334	+	0.892	0.002	29.373
		2 days	+	0.775	0.008	19.409	+	0.135	0.191	28.721	+	0.466	0.049	28.74
	Dissipation of turbulent	12 hours	+	0.938	0.001	19.503	+	0.797	0.006	31.399	+	0.937	0.001	29.388
		24 hours	+	0.879	0.002	19.481	+	0.991	0.001	31.481	+	0.903	0.001	29.378

	kinetic energy	2 days	+	0.685	0.016	19.306	+	0.46	0.051	30.805	+	0.529	0.037	28.906
BDW	Upwelling	12 hours	+	0.964	0.001	19.932	+	0.817	0.005	37.137	+	0.892	0.002	32.264
		24 hours	+	0.834	0.004	19.88	+	0.522	0.038	36.696	+	0.787	0.007	32.196
		2 days	+	0.771	0.008	19.83	+	0.182	0.156	34.999	+	0.493	0.044	31.706
	Dissipation of turbulent kinetic energy	12 hours	+	0.421	0.06	19.134	+	0.828	0.004	37.145	+	0.551	0.033	31.847
		24 hours	+	0.493	0.044	19.352	+	0.962	0.001	37.201	+	0.741	0.01	32.152
		2 days	+	0.428	0.058	19.157	+	0.355	0.078	36.144	+	0.357	0.077	31.239
BB	Upwelling	12 hours	+	0.685	0.016	22.226	+	0.568	0.031	33.839	+	0.776	0.008	30.72
		24 hours	+	0.824	0.005	22.368	+	0.905	0.001	34.224	+	0.983	0.001	30.82
		2 days	+	0.947	0.001	22.424	+	0.424	0.059	33.454	+	0.75	0.01	30.695
	Dissipation of turbulent kinetic energy	12 hours	+	0.197	0.146	20.372	+	0.802	0.006	34.166	+	0.63	0.022	30.533
		24 hours	+	0.489	0.044	21.839	+	0.557	0.032	33.817	+	0.692	0.015	30.627
		2 days	+	0.92	0.001	22.417	+	0.947	0.001	34.242	+	0.746	0.01	30.69
CR	Upwelling	12 hours	+	0.359	0.077	20.508	+	0.356	0.078	5.571	+	0.211	0.138	18.187
		24 hours	+	0.121	0.204	18.583	+	0.574	0.03	6.231	+	0.111	0.215	16.977
		2 days	+	0.34	0.083	20.422	+	0.958	0.001	6.619	+	0.46	0.051	19.445

	Dissipation of turbulent kinetic energy	12 hours	+	0.426	0.058	20.767	+	0.711	0.013	6.453	+	0.659	0.018	19.88
		24 hours	+	0.153	0.176	19.031	+	0.705	0.014	6.446	+	0.171	0.163	17.805
		2 days	+	0.275	0.107	20.079	+	0.571	0.03	6.225	+	0.412	0.062	19.291
KOS	Upwelling	12 hours	+	0.753	0.009	0.966	+	0.535	0.036	13.134	+	0.734	0.011	7.508
		24 hours	+	0.768	0.008	0.981	+	0.793	0.007	13.525	+	0.849	0.003	7.606
		2 days	+	0.903	0.001	1.07	+	0.922	0.001	13.598	+	0.921	0.001	7.639
	Dissipation of turbulent kinetic energy	12 hours	+	0.796	0.006	1.006	+	0.599	0.026	13.268	+	0.734	0.011	7.509
		24 hours	+	0.685	0.016	0.885	+	0.9	0.001	13.591	+	0.982	0.001	7.651
		2 days	+	0.185	0.154	-1.085	+	0.729	0.011	13.462	+	0.408	0.063	6.805

Upwelling had a significant positive relationship with *Perna perna* and total recruit abundances at Brighton Beach (BB) at a time lag of 1 month (Table 3.10). Upwelling explained 71,1% and 70,3% of the total variation of *P. perna* and total recruit abundances respectively. At Boardwalk (BDW), upwelling had a significant relationship with *Mytilus galloprovincialis* (lagged at 7 days, 14 days and 1 month) and total recruit (lagged at 1 month) abundances (Table 3.10). The highest explanatory power (AIC = 16.581) explained 71% of the total variation of *M. galloprovincialis* recruit abundances at a time lag of 14 days. At a 1-month time lag, upwelling explained 71.2% of the total variation of total recruit abundances.

Table 3.10: Multiple linear regression analysis showing the relationship between physical variables and recruits of each taxon at a given site over different time lags. For each relationship, +/- is the sign of the regression, p-value is the level of significance, R^2 is total variation explained and AIC indicates the Akaike Information Criterion. Significant results ($p < 0.001$) are shown in bold. SK = Skoenmakerskop, CP = Chelsea Point, BDW = Boardwalk, BB = Brighton Beach, CR = Cannon Rocks and KOS = Kenton-on-Sea.

Site	Variable	Lag	*Perna perna* recruits				*Mytilus galloprovincialis* recruits				Total recruits			
			Sign	p-value	R^2	AIC	Sign	p-value	R^2	AIC	Sign	p-value	R^2	AIC
SK	Upwelling	24 hours	+	0.804	0.006	18.404	+	0.49	0.044	27.954	+	0.584	0.028	22.194
		2 days	+	0.992	0.001	18.48	+	0.292	0.1	27.169	+	0.384	0.07	21.627
		4 days	+	0.439	0.055	17.739	+	0.171	0.163	26.226	+	0.222	0.132	20.719
		7 days	+	0.483	0.046	17.871	+	0.069	0.27	24.458	+	0.132	0.194	19.755
		14 days	+	0.144	0.184	15.841	+	0.054	0.297	23.967	+	0.027	0.373	16.488
		1 month	+	0.126	0.199	15.593	+	0.003	0.555	18.007	+	0.002	0.585	11.125
	Dissipation of turbulent kinetic energy	24 hours	+	0.563	0.031	18.067	+	0.737	0.011	28.402	+	0.59	0.027	22.206
		2 days	+	0.195	0.148	16.402	+	0.278	0.106	27.089	+	0.122	0.203	19.611
		4 days	+	0.174	0.161	16.194	+	0.421	0.06	27.742	+	0.282	0.104	21.135
		7 days	+	0.325	0.088	17.283	+	0.544	0.034	28.088	+	0.362	0.076	21.537
		14 days	+	0.209	0.139	16.529	+	0.992	0.001	28.542	+	0.521	0.038	22.056
		1 month	+	0.008	0.484	9.887	+	0.657	0.019	28.298	+	0.154	0.176	20.051

CP	Upwelling	24 hours	+	0.653	0.019	28.619	+	0.743	0.01	26.56	+	0.563	0.031	26.169
		2 days	+	0.966	0.001	28.867	+	0.414	0.062	25.867	+	0.657	0.019	26.339
		4 days	+	0.978	0.001	28.869	+	0.165	0.167	24.312	+	0.578	0.029	26.201
		7 days	+	0.841	0.004	28.82	+	0.096	0.231	23.274	+	0.471	0.048	25.941
		14 days	+	0.508	0.041	28.326	+	0.117	0.208	23.657	+	0.271	0.109	25.804
		1 month	+	0.198	0.146	26.818	+	0.009	0.476	18.295	+	0.05	0.305	21.852
	Dissipation of turbulent kinetic energy	24 hours	+	0.881	0.002	28.842	+	0.78	0.007	26.597	+	0.985	0.001	26.583
		2 days	+	0.22	0.133	27.009	+	0.384	0.069	25.757	+	0.177	0.159	24.329
		4 days	+	0.718	0.012	28.709	+	0.394	0.067	25.794	+	0.541	0.035	26.12
		7 days	+	0.933	0.001	28.861	+	0.83	0.004	26.637	+	0.847	0.004	26.537
		14 days	+	0.43	0.057	28.1	+	0.921	0.001	26.681	+	0.571	0.03	26.186
		1 month	+	0.008	0.484	20.257	+	0.35	0.08	25.614	+	0.024	0.385	20.258
BDW	Upwelling	24 hours	+	0.402	0.065	32.154	+	0.197	0.147	30.605	+	0.217	0.135	29.958
		2 days	+	0.601	0.026	32.686	+	0.124	0.202	29.736	+	0.286	0.103	30.437
		4 days	+	0.048	0.311	28.187	+	0.012	0.451	24.866	**+**	0.016	0.421	24.75
		7 days	+	0.078	0.256	29.18	**+**	**<0.001**	**0.646**	**19.172**	**+**	0.009	0.474	23.49
		14 days	+	0.019	0.409	26.185	**+**	**<0.001**	**0.71**	**16.581**	**+**	0.002	0.602	19.873
		1 month	+	0.003	0.571	22.031	**+**	**0.001**	**0.621**	**20.037**	**+**	**<0.001**	**0.712**	**16.684**

	Dissipation of turbulent kinetic energy	24 hours	+	0.872	0.002	32.992	+	0.365	0.075	31.651	+	0.799	0.006	31.765
		2 days	+	0.192	0.15	30.915	+	0.561	0.032	32.249	+	0.22	0.133	29.99
		4 days	+	0.081	0.252	29.25	+	0.294	0.1	31.303	+	0.102	0.225	28.538
		7 days	+	0.104	0.222	29.759	+	0.365	0.075	31.651	+	0.142	0.185	29.179
		14 days	+	0.117	0.208	29.985	+	0.601	0.026	32.328	+	0.198	0.146	29.795
		1 month	+	0.013	0.442	25.444	+	0.875	0.002	32.635	+	0.133	0.193	29.064
BB	Upwelling	24 hours	+	0.427	0.058	40.87	+	0.385	0.069	29.429	+	0.46	0.051	38.644
		2 days	+	0.573	0.03	41.257	+	0.029	0.364	24.486	+	0.33	0.086	38.147
		4 days	+	0.073	0.263	37.683	+	0.019	0.407	23.561	+	0.022	0.391	32.873
		7 days	+	0.056	0.293	37.142	+	0.004	0.542	20.203	+	0.017	0.419	32.267
		14 days	+	0.019	0.405	34.905	+	0.011	0.456	22.456	+	0.007	0.498	30.372
		1 month	**+**	**<0.001**	**0.711**	**25.524**	+	0.041	0.328	25.193	**+**	**<0.001**	**0.703**	**23.522**
	Dissipation of turbulent kinetic energy	24 hours	+	0.878	0.002	41.622	+	0.221	0.133	28.51	+	0.843	0.004	39.271
		2 days	+	0.265	0.112	40.113	+	0.878	0.002	30.331	+	0.192	0.149	37.215
		4 days	+	0.227	0.129	39.848	+	0.558	0.032	29.936	+	0.177	0.159	37.062
		7 days	+	0.321	0.089	40.434	+	0.742	0.01	30.226	+	0.269	0.11	37.809
		14 days	+	0.312	0.092	40.389	+	0.674	0.017	30.141	+	0.344	0.082	38.211
		1 month	+	0.041	0.328	36.492	+	0.181	0.157	28.144	+	0.22	0.133	37.462

CR	Upwelling	24 hours	+	0.106	0.219	23.731	+	0.26	0.114	19.144	+	0.09	0.239	22.572
		2 days	+	0.315	0.091	25.705	+	0.765	0.008	20.604	+	0.322	0.089	24.915
		4 days	+	0.418	0.06	26.142	+	0.912	0.001	20.7	+	0.457	0.051	25.445
		7 days	+	0.459	0.051	26.274	+	0.556	0.032	20.286	+	0.579	0.029	25.748
		14 days	+	0.443	0.054	26.225	+	0.553	0.033	20.28	+	0.577	0.029	25.744
		1 month	+	0.676	0.016	26.736	+	0.026	0.375	14.613	+	0.467	0.049	25.475
	Dissipation of turbulent kinetic energy	24 hours	+	0.994	0.001	26.952	+	0.492	0.044	20.132	+	0.936	0.001	26.121
		2 days	+	0.883	0.002	26.925	+	0.486	0.045	20.116	+	0.951	0.001	26.124
		4 days	+	0.691	0.015	26.757	+	0.711	0.013	20.546	+	0.742	0.01	25.994
		7 days	+	0.477	0.047	26.327	+	0.49	0.044	20.126	+	0.479	0.047	25.508
		14 days	+	0.998	0.001	26.952	+	0.576	0.029	20.328	+	0.959	0.001	26.125
		1 month	+	0.225	0.131	25.129	+	0.97	0.001	20.713	+	0.279	0.105	24.682
KOS	Upwelling	24 hours	+	0.475	0.047	27.933	+	0.892	0.002	30.021	+	0.63	0.022	30.667
		2 days	+	0.948	0.001	25.56	+	0.59	0.027	29.684	+	0.913	0.001	30.94
		4 days	+	0.861	0.003	28.527	+	0.702	0.014	29.862	+	0.872	0.002	30.922
		7 days	+	0.804	0.006	28.489	+	0.236	0.125	28.309	+	0.645	0.02	30.691
		14 days	+	0.58	0.029	28.186	+	0.164	0.168	27.649	+	0.415	0.061	30.134
		1 month	+	0.076	0.258	24.678	+	0.021	0.397	23.469	+	0.035	0.345	25.446

	Dissipation of turbulent kinetic energy	24 hours	+	0.908	0.001	28.549	+	0.48	0.046	29.426	+	0.694	0.015	30.763
		2 days	+	0.678	0.016	28.352	+	0.501	0.042	29.485	+	0.945	0.001	30.949
		4 days	+	0.372	0.073	27.582	+	0.631	0.022	29.759	+	0.682	0.016	30.747
		7 days	+	0.877	0.002	28.536	+	0.835	0.004	29.99	+	0.951	0.001	30.95
		14 days	+	0.495	0.043	27.99	+	0.83	0.004	29.987	+	0.641	0.02	30.686
		1 month	+	0.089	0.24	24.995	+	0.555	0.033	29.612	+	0.182	0.156	28.751

The upwelling index and the dissipation of turbulent kinetic energy had no relationship with the abundances of barnacle cyprids and juvenile barnacles at all the sites and with all the time lags (Table 3.11).

Table 3.11: Multiple linear regression analysis showing the relationship between physical variables and each barnacle ontogenic stage at a given site over different time lags. For each relationship, +/- is the sign of the regression, p-value is the level of significance, R^2 is total variation explained and AIC indicates the Akaike Information Criterion. Significant results ($p < 0.001$) are shown in bold. SK = Skoenmakerskop, CP = Chelsea Point, BDW = Boardwalk, BB = Brighton Beach, CR = Cannon Rocks and KOS = Kenton-on-Sea.

Site	Variable	Lag	Barnacle cyprids				Juvenile barnacles			
			Sign	p-value	R^2	AIC	Sign	p-value	R^2	AIC
SK	Upwelling	12 hours	+	0.28	0.105	-44.293				
		24 hours	+	0.798	0.006	-42.931				
		2 days	+	0.333	0.085	-44.009	+	0.913	0.001	16.314
		4 days					+	0.609	0.025	16.005
		7 days					+	0.566	0.031	15.922
		14 days					**+**	**0.042**	**0.325**	**11.212**
		1 month					+	0.297	0.098	14.985
	Dissipation of turbulent kinetic energy	12 hours	+	0.912	0.001	-42.866	+	0.886	0.002	16.303
		24 hours	+	0.683	0.016	-43.057	+	0.747	0.01	16.199
		2 days	+	0.778	0.008	-42.949	+	0.674	0.017	16.109
		4 days					+	0.551	0.033	15.889
		7 days					+	0.715	0.013	16.163

		14 days								
		1 month								
CP	Upwelling	12 hours	+	0.868	0.003	-9.107				
		24 hours	+	0.468	0.049	-9.724				
		2 days	+	0.493	0.044	-9.654	+	0.093	0.235	19.569
		4 days					+	0.809	0.006	22.984
		7 days					+	0.727	0.012	22.906
		14 days					+	0.595	0.026	22.708
		1 month					+	0.357	0.077	22.008
	Dissipation of turbulent kinetic energy	12 hours	+	0.328	0.087	-10.254				
		24 hours	+	0.39	0.068	-9.987				
		2 days	+	0.355	0.078	-10.131	+	0.478	0.047	22.435
		4 days					+	0.836	0.004	23.004
		7 days					+	0.301	0.097	21.733
		14 days					+	0.348	0.08	21.966
		1 month					+	0.838	0.004	23.005

BDW	Upwelling	12 hours	+	0.849	0.003	-41.071				
		24 hours	+	0.518	0.039	-41.543				
		2 days	+	0.482	0.046	-41.636	+	0.258	0.115	15.821
		4 days					+	0.204	0.142	15.413
		7 days					+	0.163	0.169	15.004
		14 days					+	0.535	0.036	16.929
		1 month					+	0.429	0.058	16.632
	Dissipation of turbulent kinetic energy	12 hours	+	0.207	0.141	-42.995				
		24 hours	+	0.524	0.038	-41.528				
		2 days	+	0.832	0.004	-41.082	+	0.393	0.067	16.502
		4 days					+	0.134	0.192	14.631
		7 days					+	0.153	0.176	14.887
		14 days					+	0.499	0.043	16.839
		1 month					+	0.321	0.089	16.19
BB	Upwelling	12 hours	+	0.091	0.237	12.481				
		24 hours	+	0.126	0.2	13.103				
		2 days	+	0.941	0.001	15.992	+	0.854	0.003	5.402
		4 days					+	0.803	0.006	5.367

		7 days					+	0.942	0.001	5.437
		14 days					+	0.874	0.002	5.413
		1 month					+	0.474	0.048	4.809
	Dissipation of turbulent kinetic energy	12 hours	+	0.149	0.18	13.42				
		24 hours	+	0.751	0.01	15.875				
		2 days	+	0.75	0.01	15.873	+	0.527	0.037	4.949
		4 days					+	0.622	0.023	5.143
		7 days					+	0.437	0.056	4.697
		14 days					+	0.807	0.006	5.37
		1 month					+	0.373	0.073	4.464
CR	Upwelling	12 hours	+	0.445	0.054	25.554				
		24 hours	+	0.261	0.113	24.716				
		2 days	+	0.116	0.209	23.225	+	0.061	0.283	27.964
		4 days					+	0.916	0.001	32.274
		7 days					+	0.641	0.02	32.018
		14 days					+	0.559	0.032	31.865
		1 month					+	0.6	0.026	31.947

	Dissipation of turbulent kinetic energy	12 hours	+	0.801	0.006	26.196				
		24 hours	+	0.667	0.017	26.046				
		2 days	+	0.425	0.059	25.488	+	0.704	0.014	32.109
		4 days					+	0.876	0.002	32.257
		7 days					+	0.306	0.095	30.993
		14 days					+	0.259	0.114	30.71
		1 month					+	0.442	0.055	31.555
KOS	Upwelling	12 hours	+	0.849	0.003	16.769				
		24 hours	+	0.961	0.001	16.811				
		2 days	+	0.524	0.038	16.312	+	0.621	0.023	25.677
		4 days					+	0.606	0.025	25.65
		7 days					+	0.37	0.074	24.986
		14 days					+	0.083	0.249	22.257
		1 month					+	0.316	0.091	24.738
	Dissipation of turbulent kinetic energy	12 hours	+	0.693	0.015	16.62	+	0.603	0.025	25.646
		24 hours	+	0.982	0.001	16.813	+	0.626	0.022	25.686
		2 days	+	0.909	0.001	16.798	+	0.411	0.0626	25.143
		4 days					+	0.491	0.044	25.394

		7 days 14 days 1 month		+	0.634	0.021	25.699

Correlation Analyses

Correlation analyses were performed to investigate whether there were any significant correlations between the number of hours of either westerly or easterly winds and the abundance of each taxon at each site. As with the multiple regression analyses, different time lags were used. For the abundance of bivalve settlers and barnacle cyprids, time lags of 12 hours, 24 hours and 2 days were used, and for the abundance of bivalve recruits and juvenile barnacles, time lags of 24 hours, 2, 4, 7 and 14 days, and 1 month were used. Due to multiple tests being done, Benjamini-Hochberg corrections were applied to minimize the occurrence of a Type I error, and the new alpha value was 0.001 (Appendix: Table A5).

Throughout all the sampling sites and lag times, there were no significant correlations between settler abundances and the number of hour of both westerly and easterly winds (Table 3.12).

Table 3.12: Correlation analysis between the number of hours of westerly and easterly wind with mussel settler abundances at a given site over different time lags. r = Pearson's correlation coefficient, and p = probability value. Significant results ($p < 0.011$) are shown in bold. Skoenmakerskop, CP = Chelsea Point, BDW = Boardwalk, BB = Brighton Beach, CR = Cannon Rocks, KOS = Kenton-on-Sea.

Site	Variable	Lag	*Perna perna* settlers		*Mytilus galloprovincialis* settlers		Total settlers	
			p	r	p	r	p	r
SK	Westerly wind	12 hours	0.623	-0.144	0.537	-0.181	0.486	-0.204
		24 hours	0.889	-0.041	0.318	-0.289	0.41	-0.24
		2 days	0.732	-0.101	0.017	-0.628	0.081	-0.484
	Easterly wind	12 hours	0.823	-0.066	0.898	0.038	0.894	-0.039
		24 hours	0.539	-0.184	0.935	-0.024	0.683	-0.12
		2 days	0.911	0.033	0.315	0.291	0.592	0.157
CP	Westerly wind	12 hours	0.677	-0.122	0.924	-0.028	0.674	-0.124
		24 hours	0.555	-0.173	0.422	-0.234	0.366	-0.263
		2 days	0.503	-0.196	0.028	-0.588	0.091	-0.471
	Easterly wind	12 hours	0.447	-0.222	0.841	-0.059	0.679	-0.122
		24 hours	0.635	-0.139	0.966	-0.012	0.851	-0.055
		2 days	0.731	-0.101	0.221	0.351	0.519	0.189

BDW	Westerly wind	12 hours	0.811	-0.071	0.282	-0.31	0.365	-.0.263
		24 hours	0.942	-0.022	0.214	-0.356	0.313	-0.292
		2 days	0.649	-0.134	0.041	-0.555	0.081	-0.486
	Easterly wind	12 hours	0.891	-0.04	0.58	-0.162	0.514	-0.191
		24 hours	0.787	0.08	0.964	0.013	0.886	-0.042
		2 days	0.526	0.186	0.209	0.359	0.397	0.247
BB	Westerly wind	12 hours	0.666	0.127	0.733	-0.101	0.754	-0.093
		24 hours	0.913	0.032	0.583	-0.161	0.633	-0.141
		2 days	0.835	0.061	0.146	-0.412	0.417	-0.237
	Easterly wind	12 hours	0.348	-0.272	0.113	-0.445	0.084	-0.481
		24 hours	0.886	-0.042	0.189	-0.374	0.204	-0.363
		2 days	0.751	-0.093	0.771	-0.086	0.363	-0.264
CR	Westerly wind	12 hours	0.141	0.416	0.547	0.177	0.17	0.391
		24 hours	0.191	0.373	0.792	-0.078	0.393	0.248
		2 days	0.709	0.11	0.429	-0.231	0.856	-0.05
	Easterly wind	12 hours	0.108	-0.451	0.511	-0.192	0.081	-0.486
		24 hours	0.062	-0.515	0.7	-0.113	0.072	-0.498
		2 days	0.489	-0.202	0.906	0.035	0.576	-0.164

KOS	Westerly wind	12 hours	0.279	0.312	0.877	0.046	0.728	0.103
		24 hours	0.212	0.357	0.629	-0.142	0.945	0.02
		2 days	0.227	0.347	0.39	-0.25	0.874	-0.047
	Easterly wind	12 hours	0.628	0.143	0.988	-0.004	0.659	0.13
		24 hours	0.771	0.086	0.918	0.03	0.823	0.066
		2 days	0.209	0.359	0.654	0.132	0.397	0.247

It is only at Boardwalk that the number of hours of westerly and easterly winds correlated with *Mytilus galloprovincialis* recruit abundances (Table 3.13). Westerly winds had a negative correlation and a correlation coefficient of -0.801 with *M. galloprovincialis* recruit abundances at a time lag of 14 days. The highest correlation coefficient (r = 0.875) explained by easterly winds were at a time lag of 14 days and the correlation was positive.

Table 3.13: Correlation analysis between the number of hours of westerly and easterly wind with mussel recruit abundances at a given site over different time lags. r = Pearson's correlation coefficient, and p = probability value. Significant results ($p < 0.011$) are shown in bold. SK = Skoenmakerskop, CP = Chelsea Point, BDW = Boardwalk, BB = Brighton Beach, CR = Cannon Rocks, KOS = Kenton-on-Sea.

Site	Variable	Lag	*Perna perna* recruits		*Mytilus galloprovincialis* recruits		Total recruits	
			p	r	p	R	p	r
SK	Westerly wind	24 hours	0.834	-0.062	0.761	-0.09	0.505	-0.195
		2 days	0.761	-0.09	0.451	-0.22	0.302	-0.299
		4 days	0.171	-0.389	0.064	-0.51	0.035	-0.57
		7 days	0.661	-0.129	0.006	-0.701	0.046	-0.543
		14 days	0.261	-0.323	0.012	-0.654	0.016	-0.637
		1 month	0.125	-0.432	0.068	-0.504	0.018	-0.624
	Easterly wind	24 hours	0.615	0.148	0.782	0.082	0.485	0.204
		2 days	0.847	0.057	0.381	0.255	0.368	0.261
		4 days	0.666	0.127	0.163	0.397	0.232	0.343
		7 days	0.885	0.043	0.062	0.514	0.18	0.382
		14 days	0.678	0.122	0.108	0.45	0.14	0.417
		1 month	0.678	0.122	0.046	0.544	0.088	0.475

CP	Westerly wind	24 hours	0.531	-0.184	0.999	<0.001	0.472	-0.21
		2 days	0.895	0.039	0.885	-0.043	0.778	-0.083
		4 days	0.564	-0.169	0.12	-0.437	0.255	-0.328
		7 days	0.915	-0.031	0.035	-0.569	0.471	-0.211
		14 days	0.605	-0.152	0.028	-0.589	0.262	-0.323
		1 month	0.041	-0.555	0.028	-0.589	0.011	-0.66
	Easterly wind	24 hours	0.204	0.363	0.897	0.038	0.26	0.325
		2 days	0.661	0.129	0.507	0.194	0.5	0.198
		4 days	0.676	0.123	0.175	0.386	0.44	0.225
		7 days	0.595	0.156	0.059	0.52	0.317	0.29
		14 days	0.728	0.103	0.12	0.438	0.382	0.254
		1 month	0.521	0.188	0.055	0.526	0.229	0.345
BDW	Westerly wind	24 hours	0.448	-0.222	0.331	-0.282	0.334	-0.28
		2 days	0.499	-0.198	0.189	-0.375	0.314	-0.291
		4 days	0.143	-0.414	0.029	-0.587	0.072	-0.499
		7 days	0.334	-0.28	0.004	-0.717	0.084	-0.841
		14 days	0.113	-0.445	**<0.001**	**-0.801**	0.018	-0.626
		1 month	0.041	-0.555	0.02	-0.617	0.015	-0.641

	Easterly wind	24 hours	0.627	0.143	0.704	0.112	0.563	0.17
		2 days	0.302	0.298	0.013	0.651	0.084	0.481
		4 days	0.1	0.461	**0.001**	**0.778**	0.017	0.631
		7 days	0.192	0.372	**<0.001**	**0.806**	0.022	0.608
		14 days	0.077	0.49	**<0.001**	**0.875**	0.006	0.704
		1 month	0.049	0.538	**0.001**	**0.772**	0.006	0.699
BB	Westerly wind	24 hours	0.769	-0.087	0.524	-0.187	0.792	-0.078
		2 days	0.861	-0.052	0.128	-0.429	0.673	-0.124
		4 days	0.252	-0.329	0.023	-0.605	0.135	-0.422
		7 days	0.245	-0.334	0.008	-0.684	0.199	-0.367
		14 days	0.1	-0.461	0.011	-0.659	0.074	-0.494
		1 month	0.017	-0.631	0.137	-0.421	0.02	-0.616
	Easterly wind	24 hours	0.445	0.223	0.741	0.098	0.598	0.155
		2 days	0.319	0.289	0.025	0.598	0.228	0.346
		4 days	0.079	0.488	0.013	0.651	0.035	0.571
		7 days	0.084	0.481	0.005	0.712	0.043	0.55
		14 days	0.046	0.543	0.003	0.735	0.022	0.61
		1 month	0.009	0.675	0.015	0.639	0.004	0.717

CR	Westerly wind	24 hours	0.164	0.395	0.529	0.184	0.154	0.404
		2 days	0.401	0.245	0.992	-0.003	0.426	0.232
		4 days	0.275	0.315	0.908	0.034	0.293	0.304
		7 days	0.356	0.268	0.46	-0.216	0.483	0.205
		14 days	0.462	0.215	0.398	-0.246	0.625	0.144
		1 month	0.76	-0.09	0.04	-0.558	0.536	-0.181
	Easterly wind	24 hours	0.501	-0.197	0.938	-0.023	0.515	-0.191
		2 days	0.837	0.061	0.293	0.304	0.747	0.095
		4 days	0.916	0.031	0.296	0.302	0.818	0.068
		7 days	0.769	0.087	0.097	0.464	0.614	0.148
		14 days	0.76	-0.09	0.241	0.337	0.924	-0.028
		1 month	0.858	0.053	0.038	0.564	0.62	0.146
KOS	Westerly wind	24 hours	0.96	-0.015	0.51	-0.193	0.804	-0.073
		2 days	0.433	-0.229	0.353	-0.269	0.382	-0.254
		4 days	0.622	-0.145	0.653	-0.132	0.655	-0.131
		7 days	0.858	-0.053	0.256	-0.327	0.66	-0.129
		14 days	0.628	-0.142	0.195	-0.37	0.439	-0.226
		1 month	0.132	-0.425	0.067	-0.505	0.072	-0.499

	Easterly wind	24 hours	0.991	0.003	0.293	0.304	0.692	0.117
		2 days	0.371	0.26	0.096	0.465	0.237	0.34
		4 days	0.486	0.204	0.213	0.356	0.392	0.249
		7 days	0.38	0.255	0.068	0.504	0.235	0.341
		14 days	0.404	0.243	0.078	0.489	0.247	0.333
		1 month	0.123	0.434	0.016	0.632	0.051	0.535

Both the number of hours of westerly and easterly winds had no significant correlation with barnacle cyprid and juvenile barnacles at all the sampling sites (Table 3.14), suggesting that the number of hours of either wind had no impact on the abundances of these groups.

Table 3.14: Correlation analysis between the number of hours of westerly and easterly wind with taxon abundance at a given site over different time lags. r = Pearson's correlation coefficient, and p = probability value. Significant results ($p < 0.001$) are shown in bold. SK = Skoenmakerskop, CP = Chelsea Point, BDW = Boardwalk, BB = Brighton Beach, CR = Cannon Rocks, KOS = Kenton-on-Sea.

Site	Variable	Lag	Barnacle cyprids		Juvenile barnacles	
			p	r	p	r
SK	Westerly wind	12 hours	0.776	-0.084		
		24 hours	0.708	0.11		
		2 days	0.171	0.389	0.93	-0.026
		4 days			0.408	-0.241
		7 days			0.225	-0.348
		14 days			0.019	-0.622
		1 month			0.325	-0.285
	Easterly wind	12 hours	0.894	-0.039		
		24 hours	0.634	-0.14		
		2 days	0.275	-0.315	0.462	0.215
		4 days			0.343	0.275
		7 days			0.428	0.231
		14 days			0.124	0.433

		1 month			0.286	0.308
CP	Westerly wind	12 hours	0.756	0.092		
		24 hours	0.524	0.187		
		2 days	0.397	0.247	0.126	0.431
		4 days			0.973	0.01
		7 days			0.367	-0.262
		14 days			0.676	-0.123
		1 month			0.667	0.127
	Easterly wind	12 hours				
		24 hours				
		2 days	0.632	0.141	0.844	-0.058
		4 days	0.907	-0.034	0.6	0.154
		7 days	0.71	-0.11	0.969	-0.011
		14 days			0.535	-0.182
		1 month			0.232	-0.343
BDW	Westerly wind	12 hours	0.958	0.015		
		24 hours	0.908	0.034		
		2 days	0.445	0.223	0.356	0.268

		4 days			0.464	0.214
		7 days			0.793	0.078
		14 days			0.826	0.065
		1 month			0.722	0.105
	Easterly wind	12 hours	0.967	-0.012		
		24 hours	0.682	0.121		
		2 days	0.884	0.043	0.614	-0.148
		4 days			0.514	-0.191
		7 days			0.435	-0.228
		14 days			0.346	-0.273
		1 month			0.514	-0.191
BB	Westerly wind	12 hours	0.584	-0.161		
		24 hours	0.621	-0.145		
		2 days	0.476	0.208	0.736	0.099
		4 days			0.9	0.037
		7 days			0.716	-0.107
		14 days			0.88	0.045
		1 month			0.668	-0.126

	Easterly wind	12 hours				
		24 hours				
		2 days	0.309	0.294	0.613	0.148
		4 days	0.39	0.25	0.691	0.117
		7 days	0.906	-0.035	0.459	0.216
		14 days			0.895	0.039
		1 month			0.384	0.253
CR	Westerly wind	12 hours	0.181	0.381		
		24 hours	0.185	0.378		
		2 days	0.242	0.336	0.194	0.371
		4 days			0.547	0.177
		7 days			0.975	-0.009
		14 days			0.381	-0.255
		1 month			0.459	-0.216
	Easterly wind	12 hours	0.431	-0.23		
		24 hours	0.5	-0.197		
		2 days	0.158	-0.401	0.301	-0.299
		4 days			0.959	-0.015

		7 days			0.783	0.081
		14 days			0.68	0.121
		1 month			0.523	0.187
KOS	Westerly wind	12 hours	0.388	-0.251		
		24 hours	0.278	-0.313		
		2 days	0.187	-0.376	0.986	-0.005
		4 days			0.873	-0.047
		7 days			0.3	-0.3
		14 days			0.108	-0.451
		1 month			0.372	-0.26
	Easterly wind	12 hours				
		24 hours	0.742	-0.097		
		2 days	0.947	0.02	0.875	0.047
		4 days	0.426	0.232	0.51	0.193
		7 days			0.334	0.28
		14 days			0.246	0.333
		1 month			0.332	0.281

3.2. Discussion

Spatial and temporal variation in wind speed and direction (Caldwell *et al*., 1986; Hsu, 1988; Schumann *et al*., 1982; Schumann & Martin, 1991) were observed in this study. Winds blowing to the east (westerly winds) dominated throughout the sampling period, increasing in frequency and speed of winds blowing to the west (easterly winds) during summer. This phenomenon of westerlies dominating throughout the year (or certainly during the sampling period, as noted in this study), and with easterly winds increasing in summer has been noted in this region previously (Schumann & Martin 1991). The delivery of larvae to the shore for settlement is controlled by factors such as the local sea breeze or wind (Hawkins and Hartnoll 1982; Kendall *et al.,* 1982; Bertness *et al.,* 1996; Pfaff *et al*., 2015), and nearshore ocean circulation in which wind has been shown to play a role (Figueiredo Jr, 1980; Winant, 1980; Ng, 1993; Capet *et al*., 2004; Woodson *et al*., 2007; Goschen *et al*., 2012).

In this study, spatial and temporal variability was, as expected (Porri et al. 2006b), noticeable for the settlers of both mussel species, *Perna perna* and *Mytilus galloprovincialis*, with high abundances of *P*. *perna* recorded at the end of summer to the end of autumn (February, March, May, and June 2018) and at the end of spring to the end of summer (October, and December 2017, and February 2018) for *M. galloprovincialis*. A similar temporal trend was notable for recruits for the two species, with low abundances at the end of winter and beginning of spring (July to September 2017) and high abundances at the end of summer into the beginning of autumn (February to April 2018). Juvenile barnacle and cyprid abundances were low during the end of winter to early summer (July to December 2017) with peak abundances over summer to the early winter months (January to June 2018). To couple these expected reproductive cycles, during the summer months, the average wind direction was either westerly (between south-west and north-west) or coming from the south (between south-west and south-east). According to the expected divergence (Marshall & Plum, 2016) and angle (Bressan and Constantin, 2019) of current direction from the wind direction, westerly winds should promote onshore currents (to the left of the wind direction) and therefore should result in an increase in settlement and recruitment of mussels and barnacles, as was observed in this study.

During the months of increased *P. perna*, *M. galloprovincialis* and overall total settler and recruit abundances, the sites located within the bay (BDW and BB) mostly presented higher abundances than those on the open coast (SK, CP, CR, and KOS). Similarly, barnacle cyprid abundances increased in numbers within the bay compared to the open coast sites. Surprisingly, in the later stage, juvenile barnacle abundances increased in numbers at SK, CP and BDW (which are the westernmost sites) rather than just within the bay. South-westerly winds might have resulted in currents moving in a north-westerly direction, due to the diversion angle caused by the earth's rotation and the Coriolis effect (Marshall & Plumb, 2016; Bressan & Constantin, 2019). The site at BDW may therefore have had statistically higher abundances than the other sites because it is located on the western side and is inside a bay, whilst the other western sites (SK and CP) are on the open coast. Cyclonic and anti-cyclonic gyres, which are normally found in bays (Dubois *et al.*, 2007), could have also resulted in larvae being trapped in the coastal boundary layer, resulting in increased settlement and recruitment at both bay sites (BDW and BB). SK, CP, and BDW are located on the western side of the study area, and with west moving currents, those sites were likely to receive more competent larvae, which would explain the increased abundance of juvenile barnacle on those sites. The increased swimming speed of cyprids (0.17–0.55 cm/s) (Chia *et al.*, 1984), could have made them more suitable to settlement on the open coast sites (SK and CP), in comparison to the slow swimming bivalve larvae (e.g., *Mytilus edulis* swimming speed of 0.11 cm/s) (Chia *et al.*, 1984). This would explain the increased abundances of juvenile barnacles, but not bivalve settlement or recruitment, on the western sites of the open coast.

Differences in the nearshore hydrodynamics at different sites with contrasting topographies can result in different settlement and recruitment abundances (Fuentes & Morales, 1994; von der Meden *et al.*, 2008). The headlands bordering an embayment influence the alongshore water flow, thereby creating a retention zone within the bay (Pitcher *et al.*, 2010). Water residence time within an embayment is higher than at an open coast site (Graham & Largier, 1997; Pitcher *et al.*, 2010; Largier, 2020). These embayments therefore increase the opportunities for retention of organisms (Roughan *et al.*, 2005; Largier, 2020) and typically increase productivity (Pitcher *et al.*, 2010; Largier, 2020).

Bays are highly productive areas, especially when located in upwelling regions (Largier, 2020). The south coast of South Africa is known for upwelling (Schumann *et al.*, 1982), and Algoa Bay, which is situated in this region, is surrounded by upwelling hotspots, namely, Cape Recife on the western side (Schumann *et al.*, 1982; 2005; Goschen & Schumann, 1995), the Agulhas Current to the south further offshore (Goschen & Schumann, 1988; Schumann *et al.*, 1988), and Cape Padrone or Woody Cape on the eastern side (Goschen *et al.*, 2012). Upwelled waters are then trapped within the bay (Goschen & Schumann, 1995; Schumann *et al.*, 2005) via cyclonic and anticyclonic circulation of currents in bays (Dubois *et al.*, 2007).

Upwelling is a phenomenon linked directly to wind forcing (McClain *et al.*, 1986; Suginohara, 1974; Capet *et al.*, 2004; Goschen *et al.*, 2012; Largier, 2020). There was no relationship between upwelling and settler abundances at any of the study sites, but there was a positive relationship with recruit abundances of *Perna perna* at one sites (BB). Similartly for *Mytilus* *galloprovincialis* settler abudances, there no relationship with any environmental variable, but upwelling positively relates with *M. galloprovincialis* recruit abundances at BDW with longer time lags (7, 14 days, and 1 month). These results suggest that increased recruitment occurred during the upwelling season. This concurs with findings of increased recruitment of mussels and barnacles around the Cape of Good Hope during the upwelling season (Pfaff *et al.*, 2011). These results indicate that early life stages respond differently to the same phenomena (such as upwelling) than the later stages, and therefore, early-stage planktonic larvae are more likely to be distributed differently throughout the water column (Tapia *et al.*, 2010; Bonicelli *et al.*, 2016). This has been demonstrated in studies of the early life stages of the marine gastropod *Concholepas concholepas*, which was concentrated at different parts of the water column than those of the later ontogenetic stage (Molinet *et al.*, 2008; Tapia *et al.*, 2010; Bonicelli *et al.*, 2016). Such patterns are likely to increase the chances of offshore transport of the early developmental stages and facilitate onshore transport of the late stages (Tester *et al.*, 2004).

Another factor that is directly linked to wind intensity is the dissipation of turbulent kinetic energy (Pringle, 2007). With an increase in wind speeds, the surface layer of water tends to be more turbulent than at the bottom (Cheung & Street, 1988). Individuals which avoid the surface are not likely to be transported by wind-driven Ekman currents near the surface, which are generated through the turbulent mixing of water (Pringle, 2007).

Persistent hours and high intensity of easterly winds generally result in upwelling along the open coast in this region (Schumann & Martin, 1991). Strong winds produce increased the dissipation of turbulent kinetic energy (Pringle, 2007). During the summer season, persistent easterly winds were noted, suggesting that there was a level of upwelling that occurred at the open coast sites around the bay. The abundance of mussel recruits positively correlated to the number of hours of easterly wind. This could be a result of increased food availability due to upwelling (Kämpf & Chapman, 2016). These strong easterly winds could have also resulted in increased turbulent kinetic energy in the water, which would also increase the feeding chances of these organisms (Marrase *et al*., 1990).

With strong easterly winds occurring between spring and autumn, it was noted that *Perna perna* started settling and recruiting after the easterlies, whilst *Mytilus galloprovincialis* settled and recruited within the period of persistent easterly winds. Barnacles, on the other hand, settled towards the end of the upwelling season towards winter. The peak settling period for both species of mussels and for barnacles could have been triggered by upwelling due to the easterly winds (Goschen *et al*., 2012), which would have resulted in an increase in food availability (Kämpf & Chapman, 2016).

Overall, the settler/recruit abundances of all the taxa studied changed over time and space as shown by the significant results of the interaction of month and site. This can be due to a number of factors, including behavioural mechanisms as well as physical processes. For example, settler/recruit abundances correlated to both upwelling and the dissipation of turbulent kinetic energy. These oceanic processes are both partly and/or mostly wind-induced/driven, as increased wind speed results in increased surface dissipation of turbulent kinetic energy. Wind direction, on the other hand, plays a role in upwelling or downwelling. The number of hours of westerly and easterly winds correlated with the early stages of mussels (settlers and recruits) and barnacles (cyprids and juveniles). Westerlies are mostly responsible for onshore surface currents, leading to downwelling, hence the increased barnacle settlement (Bertness et al., 1996), whilst easterlies are mostly responsible for offshore movement of surface currents, leading to upwelling. This directional movement of currents is responsible for larval offshore transport and onshore delivery at settlement sites.

Chapter 4

Coupling invertebrate larval distribution with settlement: consequences of the prevalent wind structures on the south-east coast of South Africa

4.1. Introduction

The movement of pelagic larvae in the water column and back to the shore to recruit into the adult population has been of interest to many researchers (Keough & Downes, 1982; Pineda, 2000; Porri *et al.*, 2006a; Pineda *et al.*, 2007; Pfaff *et al.*, 2015; Pineda *et al.*, 2018). Knowledge of larval movement increases our understanding of population dynamics (Gaines & Roughgarden, 1985), geographical species ranges (Scheltema, 1971; Broitman *et al.*, 2001; Donelson *et al.*, 2019), and the introduction and spread of invasive organisms (Geller, 1994; Pineda, 2000; McQuaid & Phillips, 2000; Thresher *et al.*, 2003; Vander Zanden & Olden, 2008). Spatio-temporal patterns of spawning and settlement of local coastal benthic populations can be linked (Fraschetti *et al.*, 2003), suggesting that the transport of larvae can be limited to the vicinity of the adult population (Prince *et al.*, 1987; McQuaid & Phillips, 2000; Tapia & Pineda, 2007). Despite coupling mechanisms between spawning and settlement, the number of individuals settling/recruiting may not directly reflect the number of larvae produced by adults (McQuaid & Lawrie, 2005; Pineda *et al.*, 2010), mostly due to the high larval loss driven by predation (Morgan, 1990; Pechenik, 1999; Johnson & Shanks, 2003; Allen, 2008), oceanic circulation (Roughgarden *et al.*, 1988; Connolly *et al.*, 2001) and pre- to post-settlement events (Fraschetti *et al.*, 2003).

To some extent, the magnitude of adult reproductive output, coupled with the direct effects of nearshore circulation, determines the availability of pelagic larvae (Connell, 1985; Roughgarden *et al.*, 1988), which in turn can influence settlement (Connell, 1985; Hurlbut, 1992; Pineda, 2000; Pineda *et al.*, 2002), as the onshore arrival of propagules has been found to be correlated with nearshore larval availability (Bertness *et al.*, 1996; Jeffery & Underwood, 2000). In line with this interdependency between larval availability and settlement, the spatio-temporal patterns of propagule distribution in the water column (Grosberg, 1982; Gaines *et al.*, 1985) and larval supply to settlement habitats (Schmitt & Holbrook, 1996;

Jenkins, 2005; Porri *et al.*, 2006a; Pineda *et al.*, 2010) are key to the structuring and dynamics of populations (Fryxell *et al.*, 2008; Nathan, 2008). To maintain populations of benthic invertebrates, competent larvae must find a suitable habitat, attach (Boyd *et al.*, 1992; Hurlbut, 1992) and eventually reproduce (Robins *et al.*, 2013).

Understanding the population dynamics of benthic invertebrates can be improved through the parallel study of larval availability and settlement (Pineda, 1991; Miron *et al.*, 1995; Pineda, 2000), as variations in benthic marine community dynamics are a result of variation in recruitment and mortality rates (Gaines & Roughgarden, 1985; Roughgarden *et al.*, 1988). Strong correlations between larval availability and settlement rates of benthic species (Minchinton & Scheibling, 1991; Miron *et al.*, 1995) can result from both biological (Marta-Almeida *et al.*, 2006) and hydrographic processes (Pineda, 1991).

The nearshore effects of circulation, influenced by physical features such as tides (Shanks, 1983; Pineda, 1999; Roegner *et al.*, 2007) and upwelling (Pineda, 1991; Shanks & Brink, 2005; Marta-Almeida *et al.*, 2006; dos Santos *et al.*, 2008), play important roles in the transport and/or retention of marine larvae (Shanks, 1986a; Townsend & Pettigrew, 1996; Morgan *et al.*, 2009; Morgan *et al.*, 2011). Wind-induced nearshore upwelling is a process whereby surface waters flow offshore (Capet *at al.*, 2004) as a result of alongshore and/or offshore winds (Schumann *et al.*, 1982; Simons, 1983; Prandle, 1987; Goschen & Schumann, 1988; Roberts, 1990; Ng, 1993; Pattiaratchi *et al.*, 1997), which also vary with time and space (Schumann & Martin, 1991). Periodic upwelling events may result in loss of larvae through offshore surface export, resulting in localized uncoupling of larval abundances in the water column and at settlement sites.

Local winds affect nearshore ocean circulation (Pruszak, 1980; Schumann *et al.*, 1982; Goschen & Schumann, 1988; Walker & Hammack, 2000; Reynolds-Fleming & Fleming, 2005;

Fontán *et al*., 2009) both in open coasts and in bays (Breitburg, 1990; Woodson *et al*., 2007; Bonicelli *et al*., 2014). Along and/or offshore wind components, leading to cross-shore currents (Guo & Valle-Levinson, 2008), may play an important role in onshore and offshore transport of material (Tyler & Seliger, 1978; Boyd *et al*., 1992), whilst the wind components responsible for clockwise and/or anti-clockwise current circulation (Kitheka, 1996; Inoue *et al*., 2000; Otobe *et al*., 2009) may result in trapping of material within a bay (Kitheka, 1996), particularly material which depends on nearshore current circulation (Shelton & Hutchings, 1982; Boyd *et al*., 1992; McQuaid & Phillips, 2000; Walker & Hammack, 2000; Roberts & van den Berg, 2005; Roberts *et al.,* 2010).

The combined design of quantifying wind effects on larval distribution in the water column (Chapter 2) and larval abundance at the settlement/recruitment sites on rocky shores (Chapter 3) warrants a further look at the relationship between larval availability with larval delivery in relation to (prevailing) winds.

4.2. Material & methods

4.2.1. Study sites

The study was conducted over four sites, namely, Cape Recife (CR) -34˚02’ S and 25°41’ E; Algoa West (AW) -34˚01’ S and 25˚43’ E, Algoa East (AE) -33˚46’ S and 26˚17’ E, and Woody Cape (WC) -33˚46’ S and 26˚19’ E, located in the nearshore, coupled with six sites, namely, Skoenmakerskop (SK; -34°02’ S, 25°32’ E), Chelsea Point (CP; -34°02’ S, 25°34’ E), Boardwalk (BDW; -33°58’ S, 25°39’ E), Brighton Beach (BB; -33°53’ S, 25°37’ E), Cannon Rocks (CR; -33°45’ S, 26°32’ E), and Kenton-on-Sea (KOS; -33°41’ S, 26°40’ E), located on the rocky intertidal zone, all of these on the south east coast of South Africa (Figure 4.1).

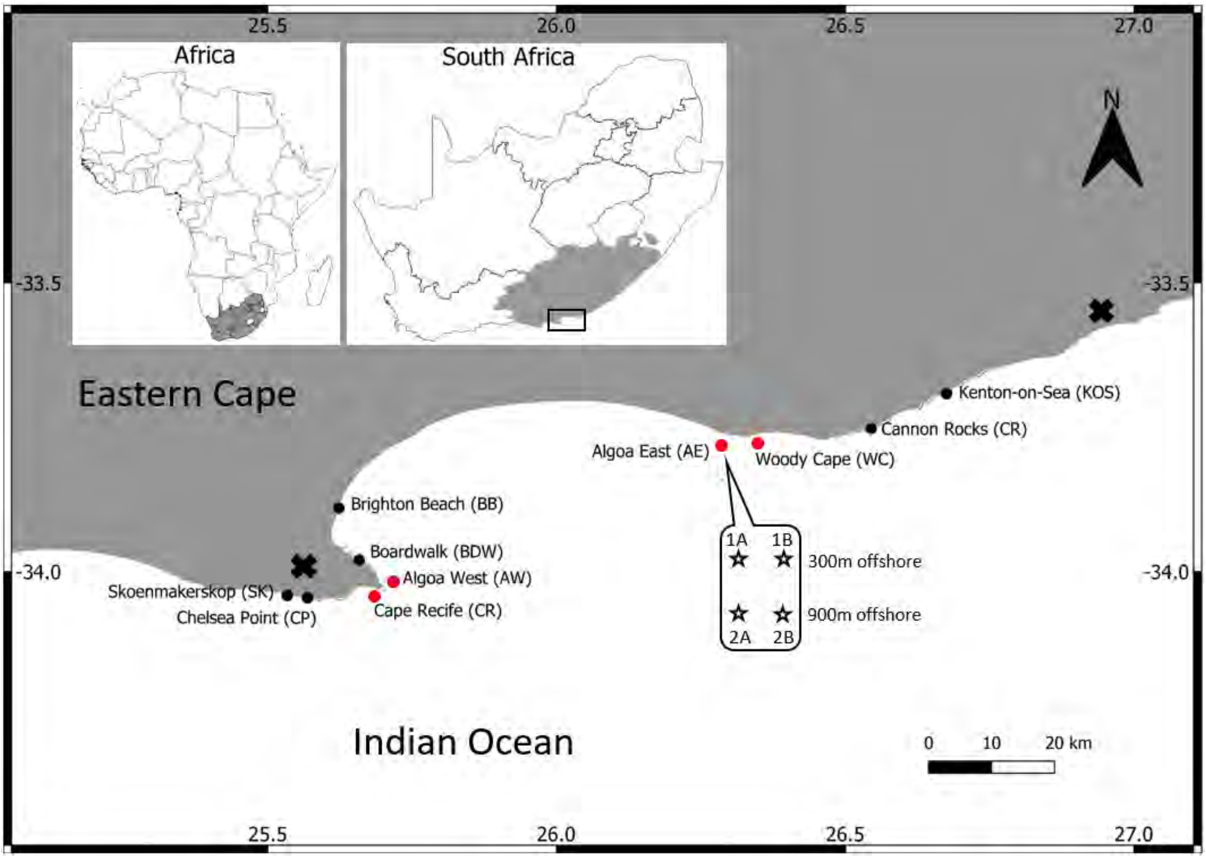

Figure 4.1: Map of the sampling sites (red and black dots represent nearshore and rocky intertidal sampling sites respectively) along the south east coast of South Africa. The stars represent the nearshore sampling design as transects (A and B) at each site and the distance of the sampling stations from the shore. The black crosses represent the Port Elizabeth (left) and the Port Alfred (right) anemometer locations.

4.2.2. Physical data

Nearshore ocean current data for the period from November 2017 to May 2018 were obtained from a moored up-facing Acoustic Doppler Current Profiler (ADCP) on the 22-metre depth contour at Cape Recife. The ADCP recorded current data every 30 minutes, sampling the water column using 21 bins of 1 metre depth. Before analysis, the quality of the data from each bin was checked, and the cut-off point for quality data was deemed to be 75% of the measurements (readings) (Pattrick *et al*, 2013), while data with a quality < 75% were regarded as bad data and therefore discarded. For each measurement, the ADCP has a value called the 'Percentage Good', which is an indication of the quality of the data stored. For example, if the moored ADCP was set to ping or measure every 5 minutes, but to save an average value for a 30-minute time period. This means that there would be six pings for a 30-minute interval. The six pings would then be averaged and if the ‘Percentage Good’ value of the six pings was < 75%, then that data were removed and labelled as bad data, however, if the average value had a ‘Percentage Good’ of ≥ 75%, then that data were labelled as good data and used in an analysis. Data quality < 75% was assumed to possibly be contaminated by large particles or organisms, and therefore these data would not represent the true nature of the currents (Gordon, 1996). Currents with good data closest to the surface (at 4 metres from the surface) were used, as they were deemed most likely to be affected by wind.

Hourly wind speed data covering the whole sampling months were obtained from ERA5 hourly data on single levels from 1940 to present website. The pixels of the data points for wind speed were extracted in respect to the coordinates of the sampling sites. Hourly wind direction data were then calculated using the proxy of wind speed (zonal and meridional) on R-studio version 2002.02.3. The equation is as follows:

*Wind direction = function(u,v){(180+atan2(u,v)*180/pi)%%360}*

Where u is the alongshore wind speed, v is the cross-shore wind speed, *atan2* returns the angle in radians for the tangent u/v, and *pi* is the items response probability.

4.2.3. Biological data

The biological data collection is discussed in detail in Chapters 2 and 3. Note that only mussel larvae in the water column were correlated with larval settlement, as there were insufficient barnacle nauplii and cyprids in the water column to allow for a correlation between them and those found on the settlement/recruitment plates. There were however, enough cyprids and juvenile barnacles on the plates to allow for such correlation analysis.

4.2.4. Statistical analyses

A pooled data approach was used in the correlation of current data with wind data, whereby only hourly data were averaged for both variables. Due to the high number of models tested, to reduce Type I errors, Benjamini-Hochberg false discovery rate correction was applied (FDR, Benjamini & Hochberg, 1995). For the period during which the larval sampling overlapped with settlement and recruitment sampling, wind stick vectors were created using RStudio (v1.2.5033) and contour plots for currents were created using Surfer v4.0. In preparing the wind stick vector diagrams, the oceanographic convention (direction towards which the wind is blowing) was used, and the data were smoothed with a low-pass filter (Goschen *et al.*, 2012), which preconditions and enables processing of data (Walters & Heston, 1982; Thomson & Emery, 2014).

For the analysis of correlations between hourly winds and currents, all the primary directions (N, NE, E, SE, S, SW, W, and NW) of wind and currents were considered, while for correlations among larval distribution, settlement and wind, only westerly (between 225° and 315°) and easterly (between 45° and 135°) winds were considered. This was done as these were the focus point of the study, and therefore hypothesized to likely be responsible for cross-shore delivery of larvae, given the orientation of the coastline and the dominant winds in the region (Schumann *et al.*, 1988; Schumann & Martin, 1991). This approach was considered as the sampling sites were perpendicular to west and east prevalent winds, and were therefore likely to receive the effect of wind from these directions in an alongshore manner. Since wind and current direction are circular data (modulo 360), a circular-circular correlation was performed (Fisher & Lee, 1983) to test whether wind direction correlated with current direction. This correlation analysis was done using Oriana v4.01.

A possible relationship between larval availability and larval settlement/recruitment was investigated by correlating the abundance of larvae in the water column with the abundance of mussel settlers/recruits collected on the scouring pads and barnacle cyprids/juveniles on the plates. The correlations were done on larvae collected on certain months, with settlers and/or recruits of the same month. Shapiro-Wilk's W test and Levene's test were used to test for normality of data and homogeneity of variance, respectively. Data were then log transformed to satisfy the normality assumption (Feng *et al*., 2014). Correlation analyses were performed using Spatial Analysis in Macroecology (v4.0).

Larval abundances in the water column and settlement pads were separately correlated with wind data. Due to low numbers of specimens per mussel taxon, larvae were pooled, and the daily sampling averages of the total larvae in the water column over both depth and distance from shore per site were correlated with the number of hours of westerly and easterly wind, as well as the average wind speed in both directions. Monthly averages of the total settlers, total recruits, total barnacle cyprids and total juvenile barnacles per site were also correlated with the number of hours of westerly and easterly wind and the average wind speed for both wind directions. Wind data were lagged by 12 hours, 24 hours, 2 days, 4 days, 7 days, 14 days and 1 month for the analysis of larval abundance in the water column, and by 12 hours, 24 hours and 2 days for the analysis of abundance of bivalve settlers and barnacle cyprids, whilst 12 hours, 24 hours, 2 days, 4 days, 7 days, 14 days, and 1-month time lags were used for bivalve recruits and juvenile barnacles. Due to the multiple tests performed, the false discovery rate correction was applied (FDR, Benjamini and Hochberg, 1995) to reduce the risk of Type I error. Pearson correlation analyses were performed on Statistical Analysis for Macroecology (SAM) v4.

4.3. Results

4.3.1. Physical data

Current data from the top three depths (1–3 m) of the water column were excluded from the analysis as they contained a high proportion of bad data (Figure 4.2 gives an example from one site, CR). Current data at 4 m depth were the closest to the surface of the water column with sufficient good data, and therefore currents from 4 m to the bottom were used for correlation analyses.

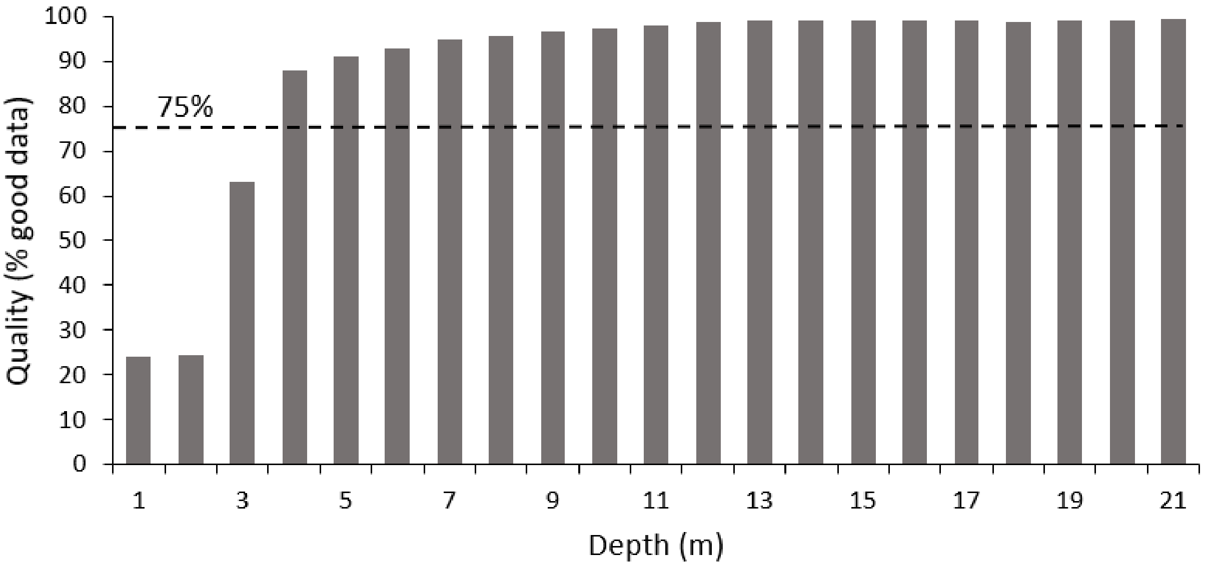

Figure 4.2: Percentage of good data at each depth from a bottom-moored ADCP found on the 22-metre depth contour in Cape Recife, on the western side of Algoa Bay. Note the low quality of data close to the surface (depth 1 to 3 metres).

After applying the Benjamini-Hochberg false discovery rate correction on the physical data of winds and currents, the new p-value was 0.023 (Appendix: Table A6).

Over the four occasions that meroplankton sampling coincided with rocky shore sampling, wind speed was significantly correlated with current speed and likewise with wind and current direction, except for wind and current speed between 2 February and 4 March 2018 at 8 m depth (Table 4.1). On three of these four occasions; 5 November to 2 December 2017, 2 December 2017 to 4 January 2018, and 2 February to 4 March 2018; wind speed was positively correlated with the current speed and had the highest correlation coefficients (r = 0.267, r = 0.218, and r = 0.193 respectively) at the deepest depth of 20 m (Table 4.1). From 4 March and 5 April 2018, the highest correlation coefficient (r = 0.145), with a positive correlation between wind and current speed was at 12 m depth.

Wind direction, on the other hand, was correlated with current direction and had the highest correlation coefficients at depths of 4 m (r = -0.095), 16 m (r = 0.083), and 16 m (r = 0.023) during three of the sampling occasions (5 November to 2 December 2017, 2 December 2017 to 4 January 2018 and 4 March to 5 April 2018, respectively). From 2 February to 4 March 2018, wind direction negatively correlated with current direction with the highest correlation coefficient (r = -0.173) at 8 m depth (Table 4.1).

Table 4.1: Correlations between wind data and nearshore current data at different depths from a moored ADCP off Cape Recife, placed at the 22 m contour. Significant correlations are shown in bold.

		Wind speed vs Current speed		Wind direction vs Current direction	
Time period	Depth	r	P	r	p
5 Nov. 2017 – 2 Dec. 2017	4 m	**0.225**	**<0.001**	**-0.095**	**<0.05**
	8 m	**0.166**	**<0.001**	**-0.032**	**<0.05**
	12 m	**0.165**	**<0.001**	**0.028**	**<0.05**
	16 m	**0.186**	**<0.001**	**0.031**	**<0.05**
	20 m	**0.267**	**<0.001**	**-0.026**	**<0.05**
2 Dec. 2017 – 4 Jan. 2018	4 m	**0.170**	**<0.001**	**-0.056**	**<0.05**
	8 m	**0.121**	**<0.001**	**0.013**	**<0.05**
	12 m	**0.124**	**<0.001**	**0.082**	**<0.05**
	16 m	**0.170**	**<0.001**	**0.083**	**<0.05**
	20 m	**0.218**	**<0.001**	**0.017**	**<0.05**
2 Feb. 2018 – 4 Mar. 2018	4 m	**0.085**	**0.023**	**0.002**	**<0.05**
	8 m	0.064	0.085	**-0.005**	**<0.05**
	12 m	**0.089**	**0.018**	**0.004**	**<0.05**
	16 m	**0.151**	**<0.001**	**0.021**	**<0.05**
	20 m	**0.193**	**<0.001**	**0.016**	**<0.05**
4 Mar. 2018 – 5 Apr. 2018	4 m	**0.108**	**0.002**	**-0.03**	**<0.05**
	8 m	**0.108**	**0.002**	**-0.003**	**<0.05**
	12 m	**0.145**	**<0.001**	**0.018**	**<0.05**
	16 m	**0.129**	**<0.001**	**0.023**	**<0.05**
	20 m	**0.122**	**<0.001**	**-0.005**	**<0.05**

The mean current velocity, as expected, decreased with depth (Figure 4.3a, b, c, d).

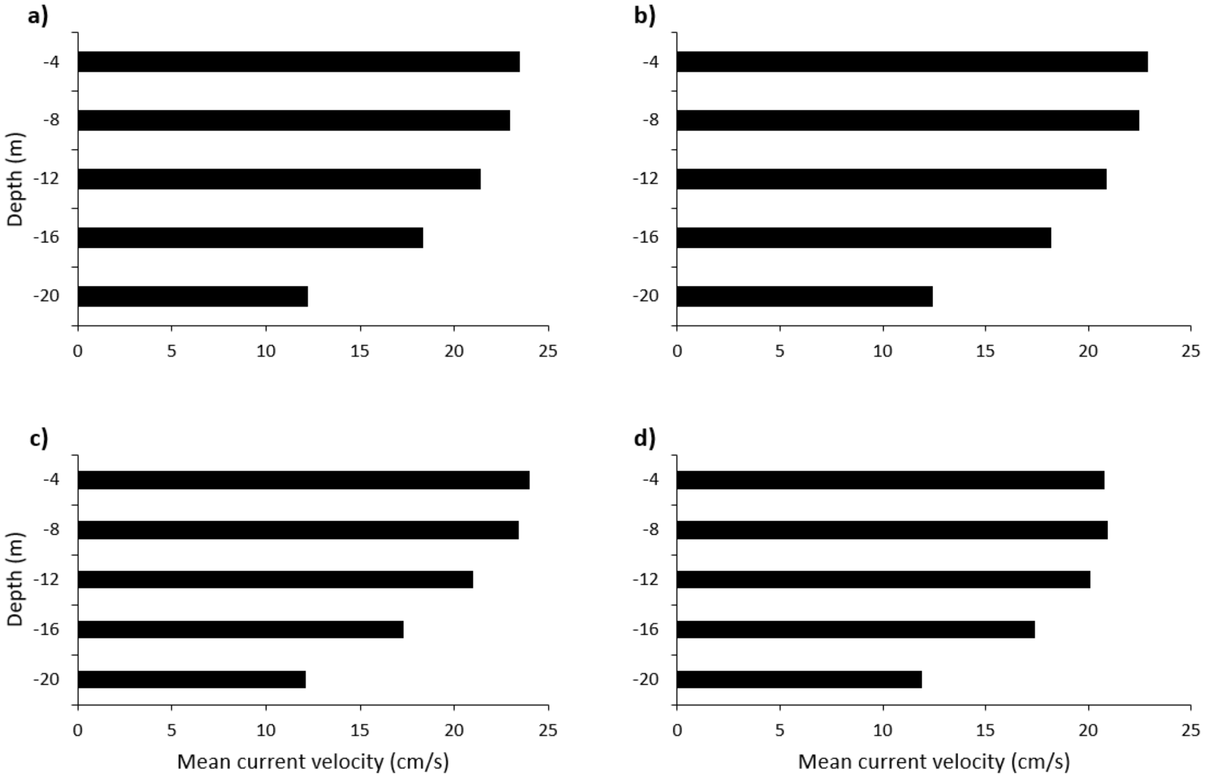

Figure 4.3: Nearshore mean current velocity at the given depth intervals during **a)** 5 November–2 December 2017, **b)** 2 December 2017–4 January 2018, **c)** 2 February–4 March 2018, and **d)** 4 March–5 April 2018 time periods. Data were collected from a bottom moored ADCP on the 22m depth contour off Cape Recife.

From 5–7 November 2017, wind blew at a velocity of 2–4 m/s to the south-east and at the same time period the current speed was between 0–30 cm/s throughout the water column (Figure 4.4a, b). During this same time period, there was vertical stratification with the surface currents moving to the east and north-east, whilst the bottom currents moved to the west and south-west (Figure 4.4c). This again was seen from 21–25 November 2017 (Figure 4.4a, b, c). From the 7–11 November 2017, when the wind blew towards the north-east direction at rates of 1–2 m/s, the current velocity was stronger (30–50 cm/s) and the currents flowed to the south-east (Figure 4.4a, b, c).

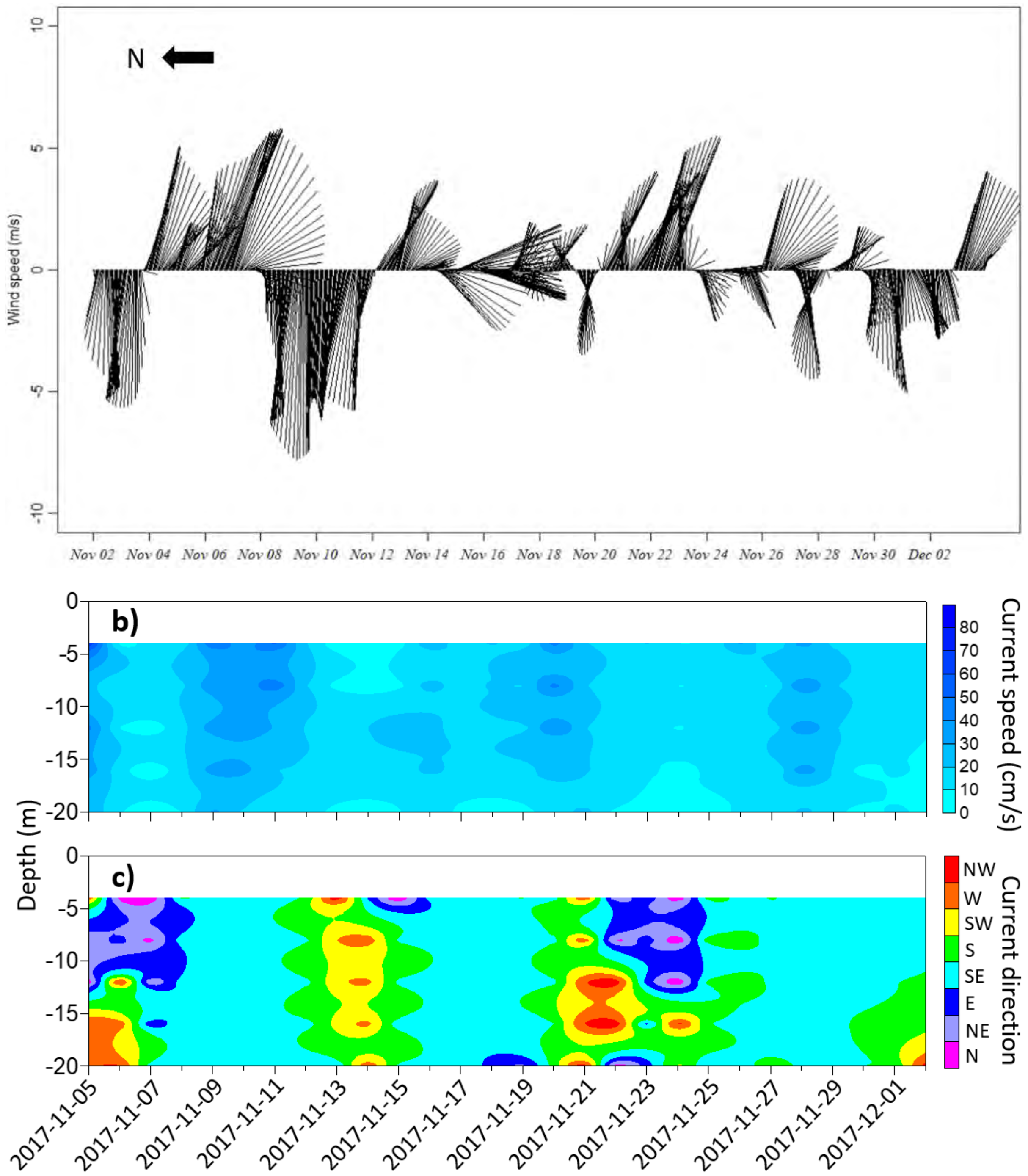

Figure 4.4: **(a)** wind data (oceanographic convention) obtained from ERA5 Reanalysis with current data; **b)** speed and **c)** direction, from a moored ADCP off Cape Recife for the time period 5 November to 2 December 2017.

During the periods of 3–9 December 2017 and 28–31 December 2017, the wind blew towards the north-east at a velocity ranging from 1–2 m/s and the currents flowed at velocities ranging from 20–50 cm/s in a south-east direction (Figure 4.5a, b, c).

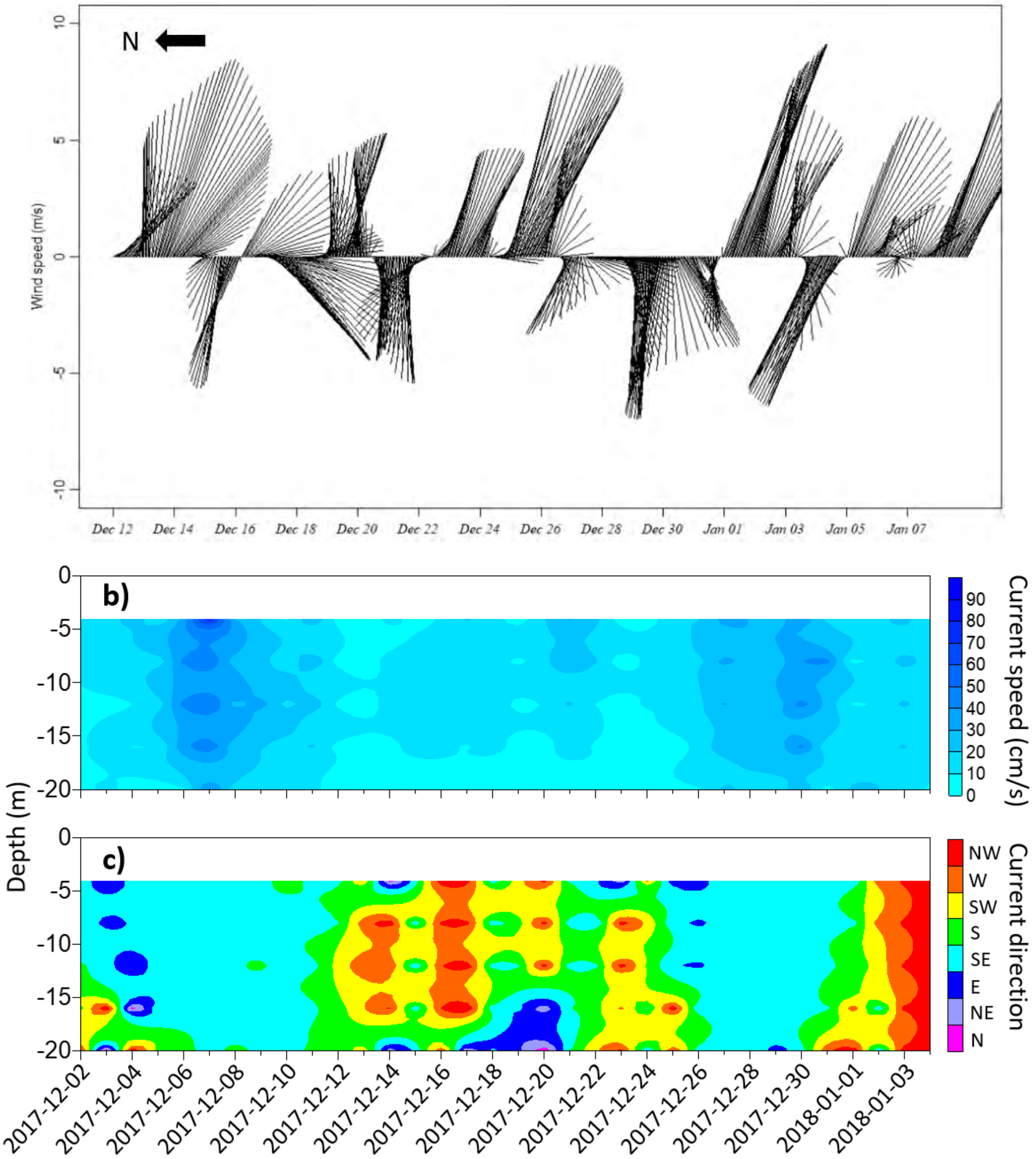

Figure 4.5: **(a)** wind data (oceanographic convention) obtained from ERA5 Reanalysis with current data; **b)** speed and **c)** direction, from a moored ADCP off Cape Recife for the time period 2 December 2017 to 4 January 2018.

From 2 February to 6 March 2018, the wind direction varied considerably, with winds alternating between blowing towards the south-east and blowing towards the north-west at speeds ranging from 1–4 m/s (Figure 4.6a). During this time, the current velocity also changed intermittently, with alternating periods of fast and slow flowing currents (Figure 4.6b). Current direction also varied, with days of homogenous currents moving to the south-east and days of currents moving in the south-west and west directions (Figure 4.6c).

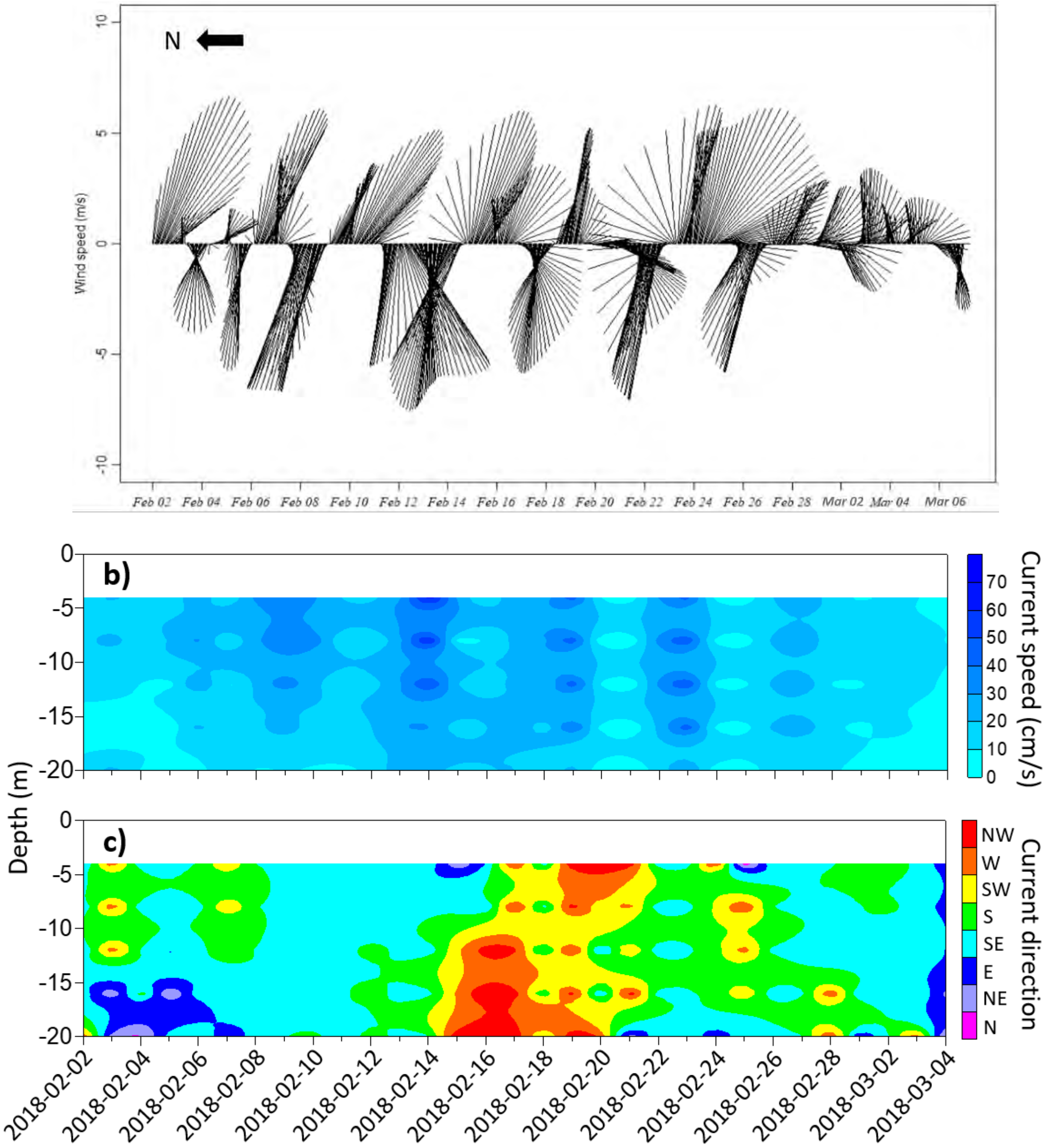

Figure 4.6: **(a)** wind data (oceanographic convention) obtained from ERA5 Reanalysis with current data; **b)** speed and **c)** direction, from a moored ADCP off Cape Recife for the time period 2 February to 4 March 2018.

During the period from 4 March to 6 April 2018, the wind varied from blowing in a south-easterly to a north westerly direction almost daily, at speeds ranging from 1–3 m/s (Figure 4.7a). The current speeds were dominated by velocities of about 10–20 cm/s (Figure 4.7b), with current directions changing from east to south-east to south to south-west, and some spikes from the west (Figure 4.7c)

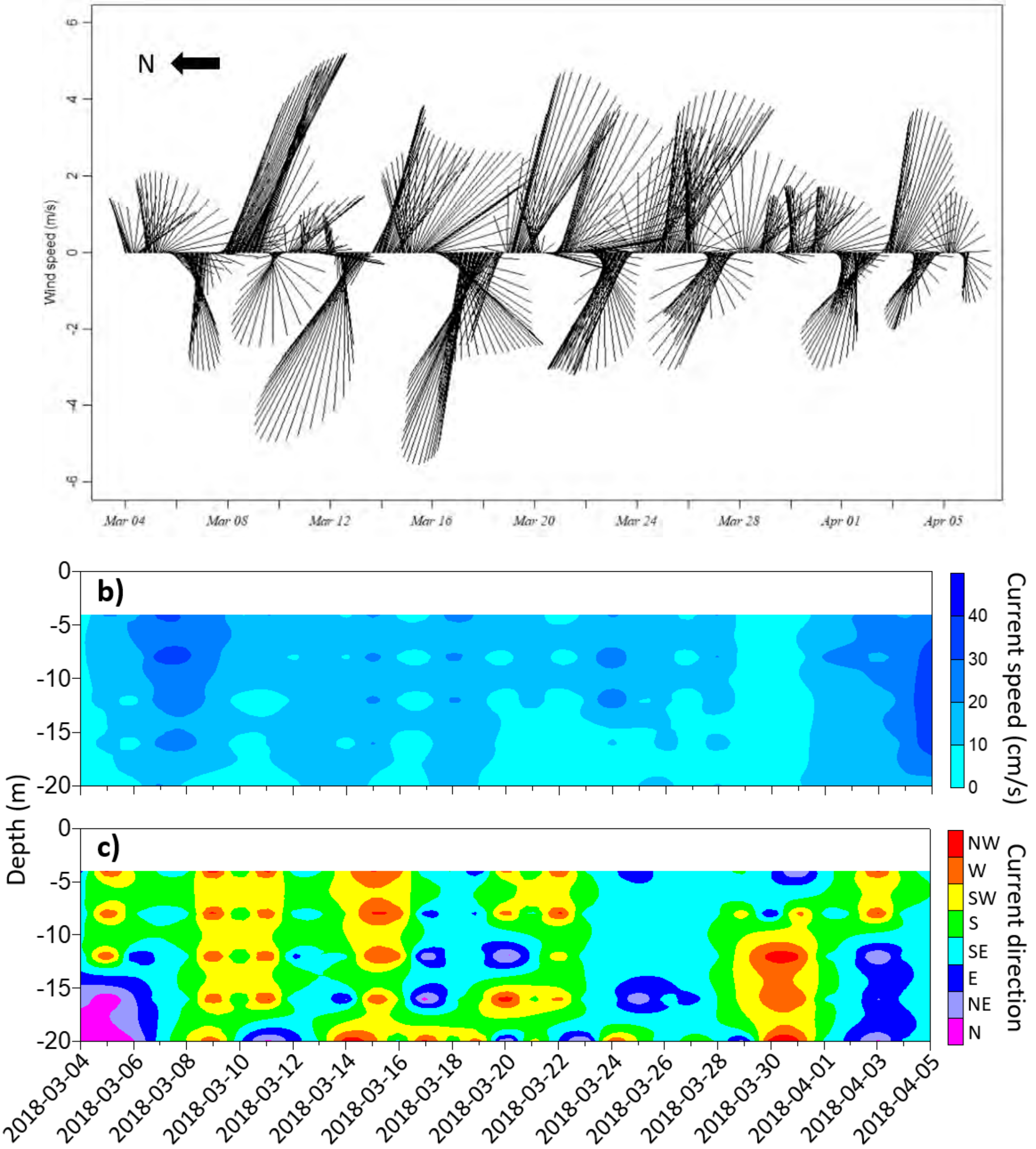

Figure 4.7: **(a)** wind data (oceanographic convention) obtained from ERA5 Reanalysis with current data; **b)** speed and **c)** direction, from a moored ADCP off Cape Recife for the time period 4 March to 5 April 2018.

4.3.2. Biological data

The average abundances of the early developmental stages (mussel settlers and barnacle cyprids, collected from pads or plates respectively) of invertebrates were positively correlated with their respective late developmental stages (mussel recruits and juvenile barnacles) (Table 4.2). In the case of mussels, the mean larval abundance in the water column did not correlate with the mean settler abundance (Table 4.2). Due to the very low numbers of barnacle nauplii or/and cyprids found in the water column, the correlation between abundances in the water column and on settlements plates was not investigated.

Table 4.2: Correlations between average mussel settler with mussel recruit abundances (n = 84), average cyprid and juvenile barnacle abundances from plates (n = 84), and the average mussel larval and settler abundances (n = 14). r = Pearson’s correlation coefficient, p = probability value. Significant results are shown in bold.

Mean mussel settler vs mean mussel recruit abundances	
r	p
0.373	**<0.001**
Mean cyprid vs mean juvenile barnacle abundances	
r	p
0.426	**<0.001**
Mean mussel larval vs mean mussel settler abundances	
r	p
-0.153	0.587

Average mussel settler abundance explained 14% of the total variation of mean recruit abundance (Figure 4.8), while the mean cyprid abundance explained 18% of the total variation in the mean abundance of the juvenile barnacles (Figure 4.9).

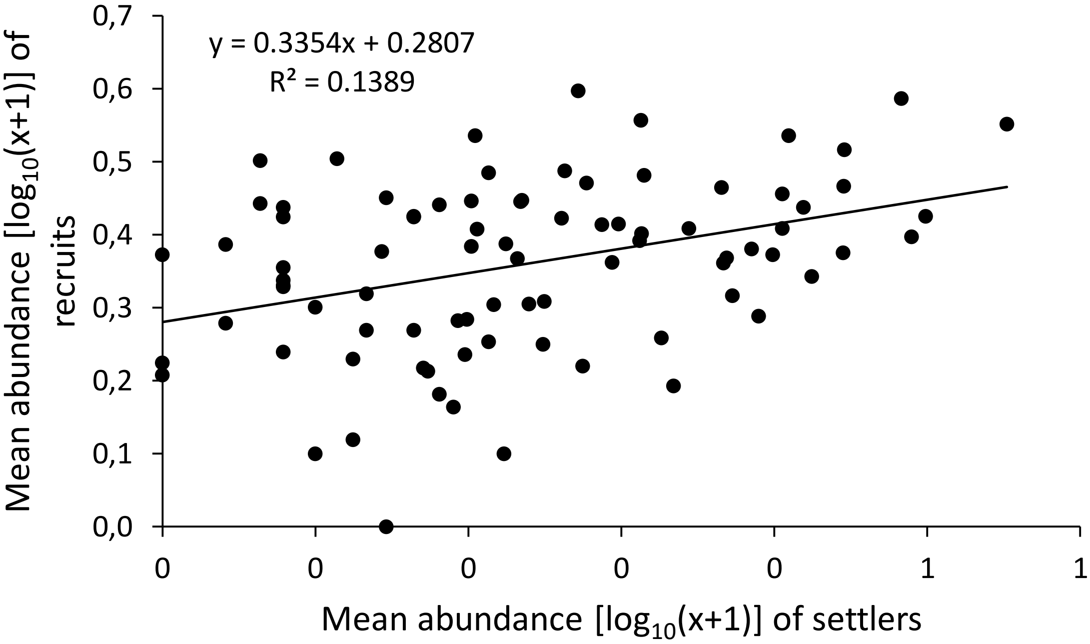

Figure 4.8: Correlation between the (log transformed) mean mussel settler and recruit abundances.

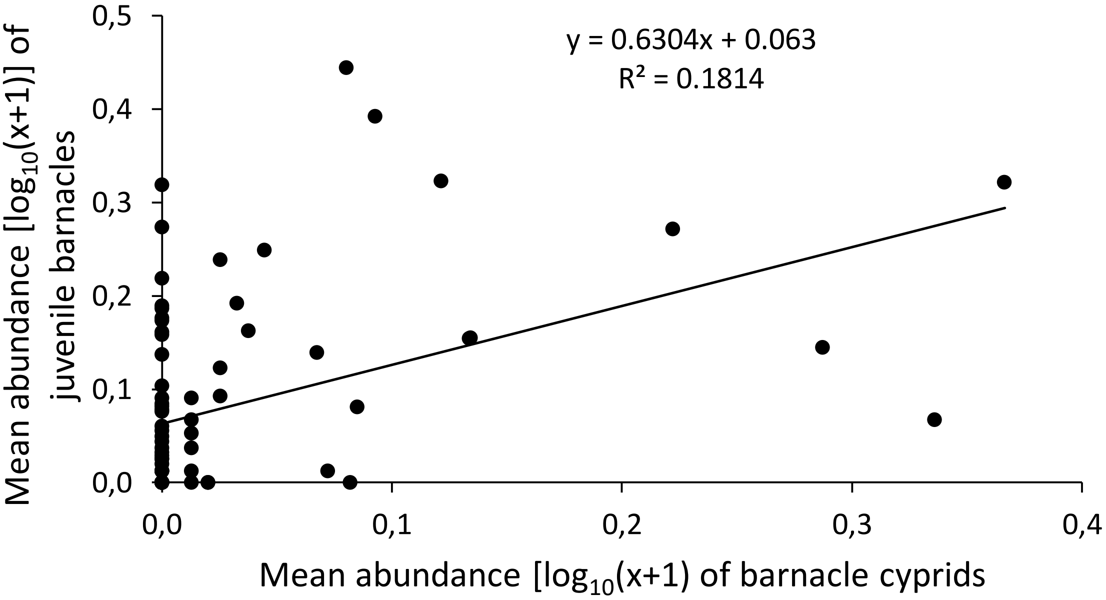

Figure 4.9: Correlation between the (log transformed) mean cyprid and juvenile barnacle abundances.

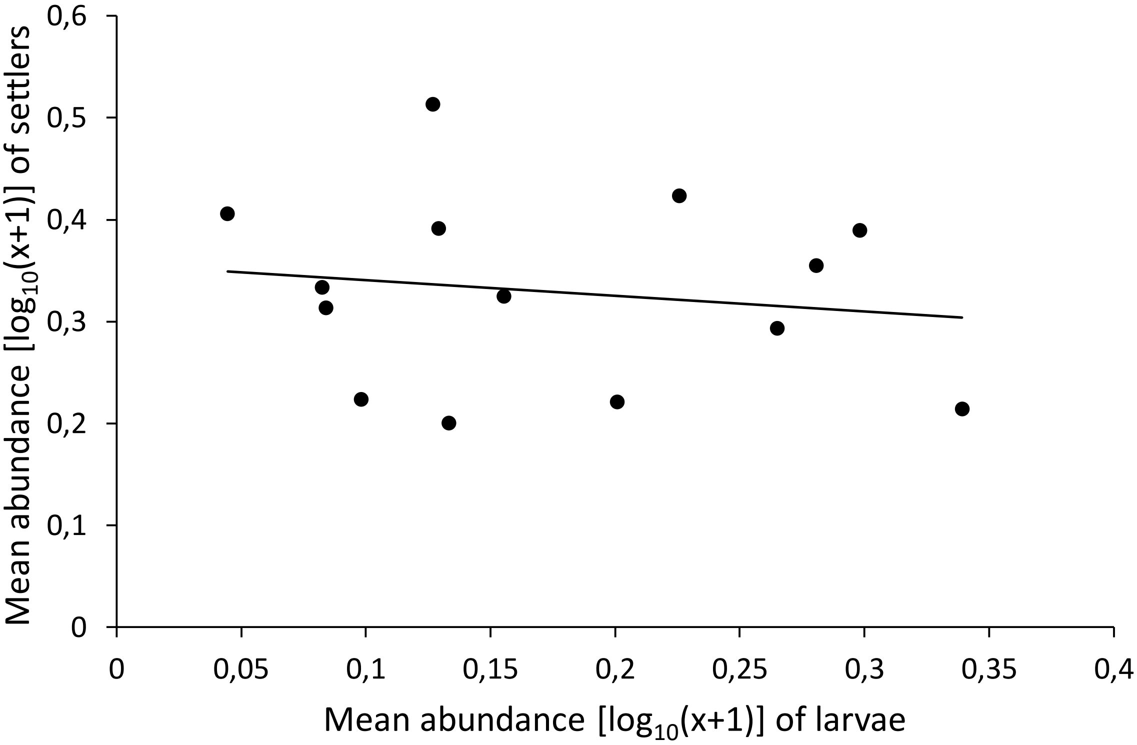

Figure 4.10: Correlation between the (log transformed) mean larval abundance in the water column and the (log transformed) mean settler abundance on the settlement pads.

4.3.3. Bio-physical relationships

With the application of the Benjamini-Hochberg false discovery rate correction to the correlation of abundance data with the number of hours and wind speed of both westerly and easterly wind, the new alpha value was 0.007 (Appendix: Table A7).

The average mussel larval abundance in the water column of all mussel taxa combined correlated positively with the number of hours of westerly wind, and negatively with the mean speed of easterly wind; both lagged at 1 month for hours of westerly and 7 and a 14-day time period for easterly wind speed (Table 4.3). The correlation coefficient was high for number of hours of westerly winds (r = 0.796). Easterly wind speeds also had high correlation coefficients (r = -0.664, and r = 0.691) for both the 7-day and 14-day time lag, respectively (Table 4.3).

Table 4.3: Correlation analysis between hours of wind and hourly average wind speeds (for both westerly and easterly) with average mussel larval abundance in the water column. r = Pearson's correlation coefficient, p = probability value. Significant results after B-H correction are shown in bold.

	Westerly hours vs abundance		Easterly winds vs abundance		Westerly speed vs abundance		Easterly speed vs abundance	
Lag	r	p	r	p	r	p	r	p
12 hours	-0.531	0.029	0.586	0.014	-0.547	0.024	0.618	0.009
24 hours	-0.482	0.052	0.427	0.089	-0.538	0.027	0.222	0.394
2 days	0.145	0.58	0.073	0.78	0.45	0.071	-0.081	0.757
4 days	-0.091	0.727	0.241	0.302	-0.254	0.325	-0.477	0.054
7 days	0.354	0.165	-0.269	0.298	-0.627	0.008	**-0.664**	**0.004**
14 days	0.5	0.042	-0.263	0.308	-0.398	0.115	**-0.691**	**0.002**
1 month	**0.796**	**<0.001**	-0.585	0.014	-0.402	0.111	-0.606	0.011

There was no correlation between the average abundance of mussel settlers and the duration and average speed of either easterly or westerly winds (Table 4.4). Duration (hours) of westerly wind however, was significantly negatively correlated with the average recruit abundance at a 14-day and 1-month time lag, with the highest correlation coefficient (r = -0.489) at a time lag of 1 month (Table 4.4). Hours of easterly wind, on the other hand, significantly positively correlated with the average recruit abundance at time lags of 2 days, 4 days, 7 days, 14 days and 1 month, with the highest correlation coefficient (r = 0.51) at a 1-month time lag (Table 4.4). The average easterly wind speed also positively correlated with the average recruit abundance at a 14-day and 1-month time lag, and the highest correlation coefficient (0.337) at a 1-month time lag (Table 4.4). It is noteworthy that the significantly highest correlation coefficients for mussel recruit abundances occurred at a 1-month time lag.

Table 4.4: Correlation analysis between hours of wind and hourly average wind speeds (for both westerly and easterly) with average mussel settler and recruit abundances. r = Pearson's correlation coefficient, p = probability value, and ns = not significant. Significant results are shown in bold.

Lag	Westerly hours vs abundance r	p	Easterly winds vs abundance r	p	Westerly speed vs abundance r	p	Easterly speed vs abundance r	p
	Average abundance of mussel settlers							
12 hours	-0.041	0.707	-0.112	0.306	-0.059	0.591	-0.112	0.308
24 hours	-0.119	0.276	-0.073	0.504	-0.08	0.469	-0.037	0.733
2 days	-0.075	0.494	-0.084	0.444	0.133	0.226	-0.092	0.4
Average abundance of mussel recruits								
12 hours	0.044	0.692	0.044	0.687	0.072	0.512	-0.003	0.978
24 hours	-0.089	0.42	0.201	0.066	0.035	0.751	0.225	0.039
2 days	-0.137	0.212	**0.29**	**0.007**	0.053	0.63	0.122	0.266
4 days	-0.166	0.131	**0.349**	**0.001**	-0.033	0.768	0.242	0.027
7 days	-0.263	0.016	**0.401**	**<0.001**	-0.042	0.706	0.289	0.008
14 days	**-0.319**	**0.003**	**0.428**	**<0.001**	-0.101	0.359	**0.298**	**0.006**
1 month	**-0.489**	**<0.001**	**0.51**	**<0.001**	-0.137	0.213	**0.337**	**0.002**

There was no correlation between hours of wind or average wind speed and the average abundance of barnacle cyprids (Table 4.5). The average westerly wind speed positively correlated with the average abundance of juvenile barnacles at time lags of 12 hours, 24 hoursand 7 days. The highest correlation coefficient (r = 0.414) was at a 7-day time lag.

Table 4.5: Correlation analysis between hours of wind and hourly average wind speeds (for both westerly and easterly) with average barnacle cyprid and juvenile abundances from barnacle settling plates. r = Pearson's correlation coefficient, p = probability value, and ns = not significant. Significant results are shown in bold.

Lag	Westerly hours vs abundance		Easterly winds vs abundance		Westerly speed vs abundance		Easterly speed vs abundance	
	r	p	r	p	r	p	r	p
	Average abundance of barnacle cyprids							
12 hours	0.063	0.57	0.025	0.824	0.09	0.416	0.116	0.295
24 hours	0.051	0.645	0.074	0.506	0.039	0.727	0.063	0.567
2 days	0.137	0.215	-0.24	0.83	0.092	0.403	0.059	0.594
Average abundance of juvenile barnacles								
12 hours	0.233	0.033	-0.125	0.257	**0.356**	**<0.001**	-0.137	0.215
24 hours	0.203	0.064	-0.023	0.837	**0.356**	**<0.001**	0.038	0.733
2 days	0.201	0.067	0.025	0.823	0.321	0.003	-0.057	0.606
4 days	0.115	0.296	0.032	0.772	0.285	0.009	0.211	0.055
7 days	-0.078	0.482	0.099	0.372	**0.414**	**<0.001**	0.192	0.08
14 days	-0158	0.152	0.129	0.243	0.179	0.102	0.217	0.047
1 month	-0.045	0.687	0.159	0.149	0.205	0.061	0.17	0.122

4.4. Discussion

A generally positive relationship between wind and current data (Table 4.1) showed that wind played a role in determining the nearshore circulation. The positive correlation between wind speed and surface current speed suggests that an increase in wind speed had a direct effect on surface currents, increasing flow velocity. The interpretation of this correlation, however, should be conservative, especially given the low correlation coefficients. There could be other factors which played a role in the speed of currents. Surface wind force is useful to some degree to estimate surface ocean velocity (Marshall & Plumb, 2016). The mean current velocities were faster (20–25 cm/s) at 4 m than at a 20 m (10–15 cm/s) depth, with a mean velocity across depths of 19–20 cm/s over the four sampling periods. Depth stratification, in terms of speed of currents, is a globally known phenomenon, with deeper layers having slower moving currents than the upper layers (Schumann *et al.*, 2005; Pattrick, 2008; Goschen *et al.*, 2012; Bressan & Constantin, 2019). A velocity gradient has been recorded from about 29 cm/s at 4 m depth to about 11 cm/s at a depth of 14 m in this bay (Pattrick, 2008) and from 70–110 cm/s at the surface to 50–55 cm/s at the bottom (Goschen *et al.*, 2012). These observations concur with the results of this study, implying that wind velocity directly affects the near-surface ocean layer, thereby increasing the current velocity closer to the surface. It is also notable that on two different occasions, the results of this study showed that wind speed also correlated with the bottom currents at 20 m, suggesting that wind could also have an effect on the flow of the bottom layer. Although surface and bottom layer currents may not be equal in velocity, my results indicate that increased wind speed and wind-driven Ekman transport, which spirals down the water column, increase the velocity of the mid-depth to near bottom layer, especially in shallow nearshore water bodies (Murray, 1970; Oliver *et al.*, 2012).

The positive correlation between wind direction and current direction (Table 4.1) is indicative that current directional flow was to some extent influenced by the wind blowing in a certain direction. With some of the low correlation coefficients, the correlation between wind direction and current direction has to be discussed with some caution, as there may be other factors affecting the current direction. It is noteworthy that some divergence occurred whereby the currents did not move in the same direction as the wind. Factors such as the wind-driven stress (currents acting in the same direction to wind), frictional force, as well as the Coriolis force (mainly caused by the earth's rotation) result in the divergence of surface current direction from wind direction (Bressan & Constantin, 2019), possibly partly explaining this mismatch between surface current direction and wind direction. In equatorial regions, the Coriolis effect due to Earth's rotation is negligible, and therefore currents flow in the same directions as the wind (Boyd, 2018). In non-equatorial regions however, the Coriolis effect comes into play, resulting in currents diverging from the direction of the wind, to the left in the Southern Hemisphere (Marshall & Plumb, 2016) with the diversion angle ranging from 30° to greater than 45° (Bressan & Constantin, 2019).

The direction of currents below the surface (between 8 m and 16 m) was, however, positively correlated with wind direction. This correlation of wind direction and nearshore ocean current direction at greater depths has been reported in this area, even down to depths of 28 metres (Goschen *et al.,* 2012). It has been noted that as water depth increases, the divergent angle of currents from the wind, caused by the Coriolis effect, increases with depth, until a certain depth where currents flow in the opposite direction to the wind, and the increase in depth results in further divergence, leading to currents flowing in the same direction as the wind (Marshall & Plumb, 2016). This depth-increase divergence might be the reason for the correlation between surface wind direction and bottom currents direction.

Marine larvae are known to be very slow swimmers, for example, *Mytilus edulis* veligers swim at speeds of about 0.11 cm/s, *Balanus balanoides* nauplii at speeds of 0.43 cm/s, and xanthid crab zoeae can swim horizontally at a speed of 2.2 cm/s (Chia *et al.*, 1984). This means that these larvae largely depend on the nearshore ocean currents for their horizontal displacement (Pineda *et al.*, 2007; Hays, 2017; Gamoyo *et al.*, 2019) and supply to adult populations (Pineda, 2000; Poulin *et al.*, 2002; Pineda *et al.*, 2010), as their swimming speed is lower than the speeds of horizontal currents of up to 90 cm/s, as seen in this study (Figure 4.4b), with a mean surface velocity of > 20 cm/s and a mean bottom velocity of > 10 cm/s (Figure 4.2a, b, c, d). The generally high correlations between the number of hours of wind from a particular direction plus the wind speeds and the abundance of larvae (Table 4.2) and recruits (Table 4.3), and the correlation between juvenile barnacles and wind speed (Table 4.4) clearly suggest that these organisms have a strong level of dependency on wind-driven nearshore ocean circulation.

These nearshore ocean currents are clearly a result of wind, as the two were, although weakly, correlated (Table 4.1). The scales of larval dispersal vary (Van Dover *et al.*, 2001) according to the amount of time spent in the water column during early development (Jenkins, 2005) and therefore larvae with long developmental times, which mostly inhabit the surface, are likely to face fast flowing currents, either onshore or offshore, depending on the wind speed and direction. Planktonic larvae with prolonged development times can have a wide dispersal range (Robins *et al.*, 2013), and mussel larvae, spending around three weeks in the water column, have been shown to have relatively limited dispersal (McQuaid & Phillips, 2000), suggesting that larval pools in the water column can supply local populations (Van Dover *et al.*, 2001).

Results from this study however, reject the coupling of mussel larval pools in the water column to the number of mussel settlers at settlement sites. This may be somehow expected given the large distance between some offshore sites and settlemement/recruitment locations. Furhtermore, hydrodynamics (Marta-Almeida *et al*., 2006; Mazzuco *et al*., 2018), larval predation due to lack of refuge in the water column (Finke & Denno, 2002), their small size (Allen, 2008) and the limited swimming speed of invertebrate larvae (Chia *et al*., 1984; Peters *et al*., 1994), lack of suitable habitat for settlement, competition for space, and spatial and temporal scales of settlement are amongst the reasons that could lead to a disconnect between larval abundance in the water column and settlement (Pineda *et al*., 2010). This study, however, found a positive correlation between larval abundance in the water column and hours of westerly wind, and a negative correlation with easterly wind speed (Table 4.2). With the currents diverging to the left in the Southern Hemisphere (Marshall & Plumb, 2016), the implication is that easterly winds should result in offshore currents (south-easterly), thereby dispersing larvae to the offshore. This could lead to larval loss, and therefore a mismatch between larvae from the water and the numbers of larvae settling on the rocky shores.

These reasons support the idea that local larval pools may not always replenish local adult populations, particularly when one considers the spatial design of this study, whereby larval samples were collected as close as possible to the settlement stations, amidst some sites where still quite a few km apart. Larval-settler uncoupling also could have been driven by a temporal mismatch in sample collections, as larval abundance and settlement were not monitored on exactly the same days. This uncoupling may also indicate that there is a time-related differential delivery of larvae (in contrast to Porri *et al*., 2006b), meaning that it is not always the local larval pool that supplies larvae to the adjacent adult community.

The average mussel settler and average recruit abundances were significantly positively correlated, as were the average abundances of barnacle cyprids and juvenile barnacles. This shows that once competent larvae are delivered to the settlement sites, the distributional pattern remains. This observation supports the idea that the delivery of larvae to the shore is the key process determining population structure, especially at these early life stages and geographical scales (Kendall *et al.,* 1982).

In conclusion, the correlation between wind and nearshore ocean currents shows that wind is one of the key factors driving nearshore ocean circulation. Nearshore hydrodynamics have been reported to play an integral part in larval distribution and supply to the settlement habitats (Porri et al. 2006a), and as shown by the correlations between larval abundances with winds in this study. This therefore suggests that wind indirectly affects larval supply to the settlement habitats, with offshore wind-driven currents resulting in low numbers of mussel settlers and recruits, thereby decoupling the relationship between larval abundance in the water column and larval abundance during settlement.

Chapter 5

The effects of early stagethermal history on the oxygen consumption rates of mussel recruits

5.1. Introduction

The biphasic life cycle of most marine benthic organisms exposes them to different environments (water as a permanent medium for larvae, and both water and air as adults, due to the tidal cycles) and this exposes the different ontogenetic stages to different physiological challenges (Shanks & Eckert, 2005). The alternate sea-land lifestyle exposes intertidal benthic organisms to extreme thermal and oxygen fluctuations (Levin *et al*., 2001) through their daily exposure to air and submersion in water (Gibson, 1986; Tagliarolo & McQuaid, 2016), making their physiological sensitivity to these alterations key to their survival (Buckley *et al*., 2001; Calosi *et al*., 2008; Pandori & Sorte, 2019). Physiological plasticity (Gibson, 1986; Anger, 1995; Helmuth, 1998; Whiteley & Mackenzie, 2016) is important, especially for the transition from the early life stages, when larvae switch for the first time in their lives from water to intertidal settlement on the rocky shore (Marshall & Morgan, 2011). This transition exposes organisms to highly variable temperatures, compared to the more constant temperatures in the water column (Sinclair *et al*., 2006; Rock *et al*., 2009), which suggests that this period is the most vulnerable of the early life stages (Anger, 2016).

Ultimately, exposure to such intertidal environmental fluctuations leads to changes in organismal physiology, and steers community composition and ecosystem functioning (Parmesan & Yohe, 2003; Pörtner & Knust, 2007; Chen *et al*., 2011). The physiological performance of early life stages during this transition phase can provide a reliable determinant of species distribution patterns (Somero, 2002) and for the adults, their tolerance to physical stressors (Pörtner & Knust, 2007; Pörtner & Farrel, 2008; Horodysky *et al*., 2015).

Environmental changes such as climate warming can shape species distribution and influence geographic shifts (Peterson *et al*., 2002; Parmesan & Yohe, 2003; Root *et al*., 2003; Perry *et* *al.*, 2005; Cheung *et al.*, 2011; Chen *et al.*, 2011). Range shifts may easily disrupt connectedness among populations and may even result in localized extinctions (Peterson *et al.*, 2002; Root *et al.*, 2003) or they may facilitate expansion by making new areas habitable (Cheung *et al.*, 2009). Understanding the environmental conditions that can potentially influence range shifts, community composition, ecosystem functioning and organismal responses to environmental conditions might be key to marine ecology (Pörtner & Knust, 2007; Horodysky *et al.*, 2015; Buckley & Huey, 2016; Pandori & Sorte, 2019).

Global changes in environmental conditions such as increased sea and air temperatures (Dickinson & Cicerone, 1986; Przeslawski *et al.*, 2008) have been recorded, modelled and predicted for the foreseeable future (Caldeira & Wickett, 2003; Feely *et al.*, 2004; Caldeira & Wickett, 2005). Such changes already affect seasonal patterns of temperature (Ernakovich *et al.*, 2014), affecting animal communities in intertidal ecosystems (Poloczanska *et al.*, 2008). These environmental changes also impact marine organisms (Mora & Ospína, 2001) by affecting cell functions (Somero, 1969), as well as rates of reproduction, growth and mortality (Brey, 1995), which could lead to changes in population density and distribution patterns and the composition of communities (Wilson, 1981), thereby altering ecosystem functioning (Glynn, 1988).

Daily to seasonal fluctuations of temperature require ongoing physiological adjustments of organisms (Jansen *et al.*, 2007; Jimenez *et al.*, 2015), as temperature is a major determinant of physiological rates (Somero, 2002; Sinclair *et al.*, 2006). Any persistent adjustment (increase or decrease) in environmental temperature can significantly influence the metabolism (metabolic rates: Gillooly *et al.*, 2001; Sinclair *et al.*, 2006; Schulte, 2015) of an organism (Dadras *et al.*, 2016), hence temperature plays a vital role in many biological processes (Huey & Bennett, 1990; Woods, 1999; Gillooly *et al.*, 2001). Adjustments in behaviour, acclimation, and heat stress among others, increase the ability of organisms to grow, reproduce (Light, 1972) and persist in physiologically challenging environments (Huey & Bennett, 1990). Such physiological adjustments resulting from metabolic rate changes are pivotal to ecological patterns, such as individual growth and feeding rates, population growth, ecosystem structure, and productivity (Brown *et al*., 2004).

Respiration, measured as oxygen consumption, is a widely used tool to estimate metabolic rate (Davis, 1975) and it can be used to determine physiological plasticity of organisms in response to thermal stress (Perry *et al*., 2005; Cheung *et al*., 2011; Tagliarolo & McQuaid, 2015). It is universally recognized that a change in temperature results in a corresponding change in the metabolic rate of organisms (Clarke, 2006; Sinclair *et al*., 2006). Due to this tight link between temperature and metabolic rate (Clarke, 2006), the correlation between environmental temperature and species distribution is easily visible, especially for organisms whose body temperatures may vary widely on seasonal and tidal cycle scales (Helmuth, 1998; 1999).

Amid the dramatic changes in temperature on the rocky intertidal zone, physiological strategies used by organisms settling in this environment are complicated and still poorly understood (Gracey *et al*., 2008; Widdicombe & Spicer, 2008; Pankhurst & Munday, 2011). Among other factors, this is a result of different and complicated physiological responses among taxa (Pörtner & Knust, 2007; Pörtner & Farrel, 2008; Horodysky *et al*., 2015), as well as each organism's thermal life-history and the prevailing environmental conditions to which they are exposed during ontogenetic development (Small *et al*., 2015). Thermal history (as larval experience), environmental change (during the transition from larvae to adult) experienced by the early life stages (Marshall, 2008; Marshall *et al*., 2008), and the rate of temperature change all play a vital role in the physiological differences among and within species and populations (Gracey *et al*., 2008; Peck *et al*., 2014). In general, the physiological adaptations of adult crustaceans have been well documented (e.g., Bliss & Mantel, 1968; Whiteley *et al*., 1997; Lagerspetz & Vainio, 2006; Lockwood & Somero, 2011; Fly & Hilbish, 2013; Thyrring *et al*., 2015), whilst physiological adaptation during the transition period between totally aquatic life stages to an intertidal benthic stage is poorly documented (Anger, 1995; Anger, 2016).

The aim of this study was to investigate whether (early stage) thermal history affects the sensitivity or tolerance of the transitional stages of mussels (settlers and recruits) on the south east coast of South Africa. Upon settlement, settlers and recruits are likely to be exposed to the extremely variable daily temperatures in the intertidal zone (Befus *et al*., 2013) which directly affects their metabolism (DeLong *et al*., 2017). With a more constant temperature in the aquatic environment as compared to the intertidal environment, the tested hypothesis was that metabolic sensitivity to temperature would decrease from settlers to recruits. In addition, temperature sensitivity was tested from month to month so as to understand how these early life stages acclimatize to different daily and monthly conditions.

5.2. Materials and Methods

5.2.1. Study sites

The transitional stages (settlers, ≤ 400 µm; and recruits, > 400 µm) of the mussels (*Perna perna* and *Mytilus galloprovincialis*) were collected during daytime low tides at four sites along the south east coast of South Africa (Figure 5.1), which corresponds to some of the same areas where settlers and recruits were collected for the studies described in the settlement/recruitment chapter (Chapter 3), namely, Brighton Beach (BB), Boardwalk (BDW), Chelsea Point (CP), and Skoenmakerskop (SK).

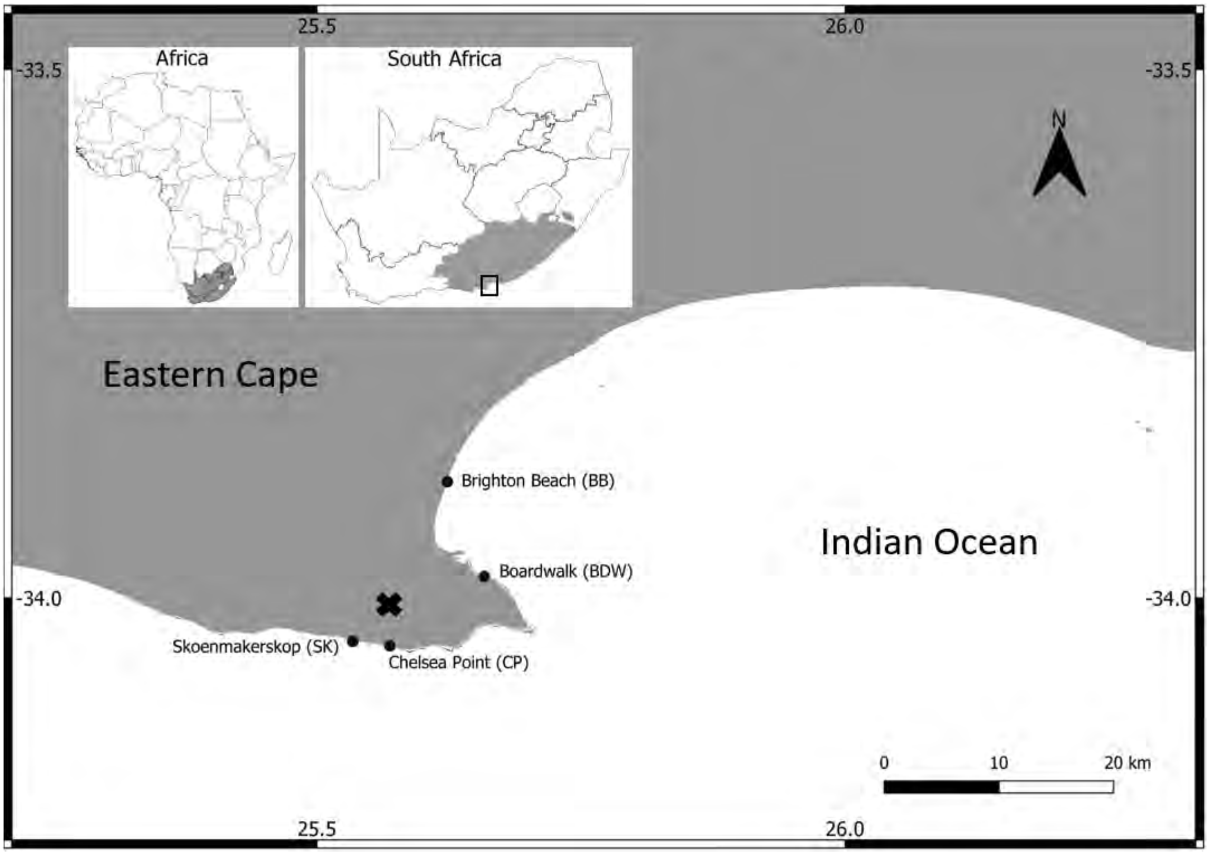

Figure 5.1: Map showing the sampling sites (black dots) along the south east coast of South Africa. The black cross represents the anemometer location.

5.2.2. Biological sampling

At each site, 10 plastic scouring pads attached to eyebolts using cable ties were placed in spaces at least 1 m apart within natural clearings in adult mussel beds, as collectors (Porri *et al.*, 2006a, b; 2007; Bownes *et al.*, 2008; Bownes & McQuaid, 2009). Two sites, one on the open coast (Skoenmakerskop) and one within the bay (Brighton Beach) were sampled during each full moon, and the other two sites, one on the open coast (Chelsea Point) and one within the bay (Boardwalk) were sampled on each new moon. This alternate collection method was used in order to be able to logistically manage the collection (keeping with the low tide), and to manage the processing and laboratory experimental runs. Due to logistic constraints such as high wave action, the month-long periods between samples did not necessarily include precisely the same number of days, and varied between 23 to 39 days per time period.

After each sampling occasion, all the collectors from the same site were kept in a single container, separate from the collectors from the other site. Each container was filled with seawater and was transported to the laboratory for further processing. Field seawater was collected in 25 L drums from the site of collection on the same day, and the temperature within the mussel beds was recorded on-site during each visit using a thermocouple (four temperature readings taken during every sampling occasion). Additionally, at each site, three temperature loggers (ibuttons) attached to eyebolts were placed within the mussel beds close to where the artificial collectors were placed. The temperature loggers were placed and replaced concurrently with the placement and replacement of the artificial collectors and were used to determine the minimum, average and maximum temperatures that settlers and/or recruits might have been exposed to. These depended on how long the organisms would have been on the collectors, being 2 days for settlers (Bownes *et al.*, 2008) and the entire month for recruits, prior to collection.

5.2.3. Experimental setup

Immediately on return to the laboratory, samples were taken to a controlled environment room at the Aquatic Ecophysiology Research Platform (SAIAB, Makhanda, South Africa) and maintained at the same temperature recorded at collection in the field. Variable numbers of collectors for each month and site were unravelled and gently washed to remove settlers and recruits in order to gather sufficient specimens to run the respiration trials. The debris resulting from the washing process was poured through a 65 µm mesh sieve, then the contents collected in the sieve were poured into a petri-dish and examined under a dissecting microscope. Mussel settlers and recruits were gently picked out using a pipette and placed in a second petri-dish. This process took at most 2 hours. The petri-dish was then placed at the bottom of a 2 L plastic tub containing filtered (using 0.45 milli-micron filter paper) seawater in a temperature-controlled room, with the temperature set at the field temperature during collection, and left overnight (approximately 12 hours).

The next day, acclimatised specimens were individually placed in the small-volume static respirometry chambers of a 24-chamber glass microplate (Loligo Systems) with volumes of 80 µl (for settlers) and 200 µl (for recruits). Each chamber on the microplate contained a non-invasive sensor spot at the bottom. Individual oxygen consumption was determined by measuring the change in oxygen concentration within each chamber between the beginning and the end of a trial. Oxygen concentration was determined optically, using the luminescent sensor spot located in each chamber, which interfaced directly with a 24-channel microplate reader (SDR Sensordish® Reader; PreSens Precision Sensing GmbH) and was connected to a laptop running the SDR software. The microplate was housed in a water bath which maintained the temperature at either the minimum, average or the maximum temperature, separately for each temperature, for 2 days prior to collection for settlers and 1 month for recruits, as recorded by the temperature loggers (with variation not exceeding ± 0.5°C) at each given site (Table 5.1).

Table 5.1: The monthly variability in water temperature ranges as well as the experimental water temperatures for the number of settlers and recruits tested at each site on a given date. BDW = Boardwalk, CP = Chelsea Point, SK = Skoenmakerskop, and BB = Brighton Beach.

Dates	Sites	Min–Max temp. (°C)	Experimental temp. (°C)	No. of settlers	No. of recruits	Total (settlers & recruits)
08-01-2019	BDW	16–28	16	0	0	0
			22	18	0	18
			30	18	0	18
09-01-2019	CP	16–28	16	9	3	12
			22	14	4	18
			30	14	2	16
23-01-2019	SK	15–29	15	0	10	10
			22	0	16	16
			30	0	18	18
24-01-2019	BB	16–30	16	0	20	20
			23	0	19	19
			30	0	13	13

06-02-2019	BDW	15–29	15	0	20	20
			22	0	18	18
			30	0	20	20
07-02-2019	CP	11–31	11	0	16	16
			21	0	20	20
			30	0	20	20
08-02-2019	BDW	15–29	15	0	19	19
			22	0	20	20
			30	0	19	19
22-02-2019	BB	15–31	15	0	16	16
			23	0	17	17
			30	0	8	8
07-03-2019	BDW	14–26	14	0	19	19
			20	0	20	20
			30	0	7	7
08-03-2019	CP	11–27	11	0	16	16
			19	0	19	19
			30	0	19	19
22-03-2019	SK	10–28	10	0	7	7
			19	0	8	8
			30	0	9	9
06-04-2019	BDW	15–27	15	10	6	16
			21	6	14	20
			30	1	0	1
08-04-2019	CP	10–26	10	0	9	9
			18	0	7	7
			30	0	9	9
19-04-2019	SK	13–25	13	1	8	9
			19	1	8	9
			30	1	4	5
20-04-2019	BB	13–29	13	0	19	19
			21	0	20	20
			30	0	15	15

5.2.4. Laboratory experiments

Prior to running each trial, settlers and/or recruits were allowed to acclimatise in a beaker at the testing temperature, for about 90 minutes. This was accomplished by placing the beaker in a water bath set at the field temperature and ramped (up or down) at 5°C per 30 minutes (0.17°C/min) (Tagliarolo & McQuaid, 2015) until the desired testing temperature was reached. Once the desired temperature was reached, the beaker with mussel settlers/recruits was left in the water bath for at least 20 minutes for further acclimation at the desired testing temperature before being taken out for the experimental run. Due to the sparsity of animals during some months, there were not always 20 individuals to place in the chambers of the microplates and therefore trials were run with the number of animals available (max 20 per temperature, per site, per time). Settlers/recruits were then individually placed in chambers as quickly as possible and if there were enough animals (n = 20), a further four chambers were left empty to provide a control for bacterial respiration. The control chambers were filled with the same filtered seawater used to fill the chambers in which settlers/recruits were placed. The microplate was then gently covered with a sheet of parafilm the same size as the microplate, followed by a rubber layer and a weight, to create an oxygen impermeable seal over the entire plate. Thereafter, the microplate was placed on top of an SDR reader inside a temperature-controlled incubator. The temperature-controlled incubator was covered with an aluminium sheet to prevent light entering and oxygen production by phytoplankton. Water flow through the water bath was used to ensure consistent temperatures in the incubator throughout the duration of each trial. Each trial at a given temperature was allowed to run for 90 minutes or a time until a 70% oxygen saturation was reached (Vorsatz *et al.*, 2021). After each trial, settlers/recruits were individually preserved in eppendorf tubes filled with 100% ethanol for later measurements necessary to calculate biovolumes, which were needed to establish the exact net volume of seawater left in the chamber after inserting the settler/recruit. The biovolumes of the settlers and recruits were calculated using an equation for a half-elliptic prism (Sun & Liu, 2003):

$$V = \frac{\pi}{4} * a * b * c$$

Where V represents the volume of organism, π is a ratio of a circumference to its diameter (constant = 3.14159), a represents the length, b represents the width, and c represents the breadth.

5.2.5. Calculation of oxygen consumption and statistical analyses

The first ten minutes of each measurement were discarded from any following analysis as that time accounted for the acclimation of settlers/recruits to the chambers, and it was the approximate time after which stabilisation or a steady decrease in oxygen was reached. Concentration readings below 70% oxygen saturation values in the testing chambers with a settler or recruit were discarded (Vorsatz *et al.*, 2021). Oxygen consumption (MO_2) was then calculated using the formula:

$$MO_2 = \frac{\Delta O_2 * vol}{t}$$

where ΔO_2 is the decrease of oxygen concentration in the water, vol is the net volume of the water in the respirometer chamber (l) after the settler/recruit was inserted, and t is the total time taken to consume 70% of oxygen from the water.

The oxygen consumption values from the control chambers were subtracted from the oxygen consumption values for each individual to account for background bacterial respiration. The amount of oxygen consumed per individual was standardised by multiplying the oxygen consumed per minute with the net volume in the chamber to achieve the exact amount of oxygen consumed by the individual per litre per minute.

Due to very low numbers of *Mytilus galloprovincialis*, it was not possible to test the difference in oxygen consumption between *Perna perna* and *M. galloprovincialis*, hence species were pooled. Due to limited numbers of settlers available among the sites and throughout the sampling months, only a single month (April 2019) at one site (BDW) was used to test whether there was a difference in oxygen consumption between settlers and recruits. For these data, a 1-way Permanova (permutational analysis of variance) was used to investigate the effect of ontogenetic stage (settler or recruit) on oxygen consumption for the month of April 2019. As there was no significant difference (p = 0.085) in oxygen consumption between the two ontogenetic stages, they were pooled (and referred to as recruits hereafter) for analysis. Months and sites were separated because temperature values were different among sites within the same month, and also different for each month within sites. Multiple 1-way permanovas were therefore performed to investigate the effects of temperature on oxygen consumption of recruits in each month/site combination separately. Only the significant results are shown for each site and month. Due to the need to perform multiple tests, Benjamini-Hochberg correction for false discovery rate was applied to reduce the possibility of a Type I error. Pairwise t-tests were run for the significant results to identify possible homogenous groups.

5.3. Results

The new alpha value after Benjamini-Hochberg correction was 0.005 (Appendix: Table A8). Only significant results from each site and month are given and the results are presented from west to east according to the site layout (from Skoenmakerskop, Chelsea Point, Boardwalk, and finally Brighton Beach). Within each site, monthly reporting of results follows.

Skoenmakerskop (SK)

There was a significant effect of temperature on the oxygen consumption of recruits in January 2019 (Table 5.2), where the average oxygen consumption at the maximum temperature was statistically higher than at the average and the minimum values (Figure 5.2).

Table 5.2: A 1-way permanova examining the effects of temperature on the oxygen consumption of recruits collected at Skoenmakerskop in January 2019. Degrees of freedom (df); Sum of Squares (SS); Mean Squares (MS); pseudo-F-ratio (Pseudo-F); permutational p-value [P(perm)]; number of permutations (Unique perms); and p-value of Monte Carlo test [P(MC)] are shown.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Temperature	2	13405	6702.5	8.7661	0.001	998	0.001
Residual	44	33642	764.59				
Total	46	47047					

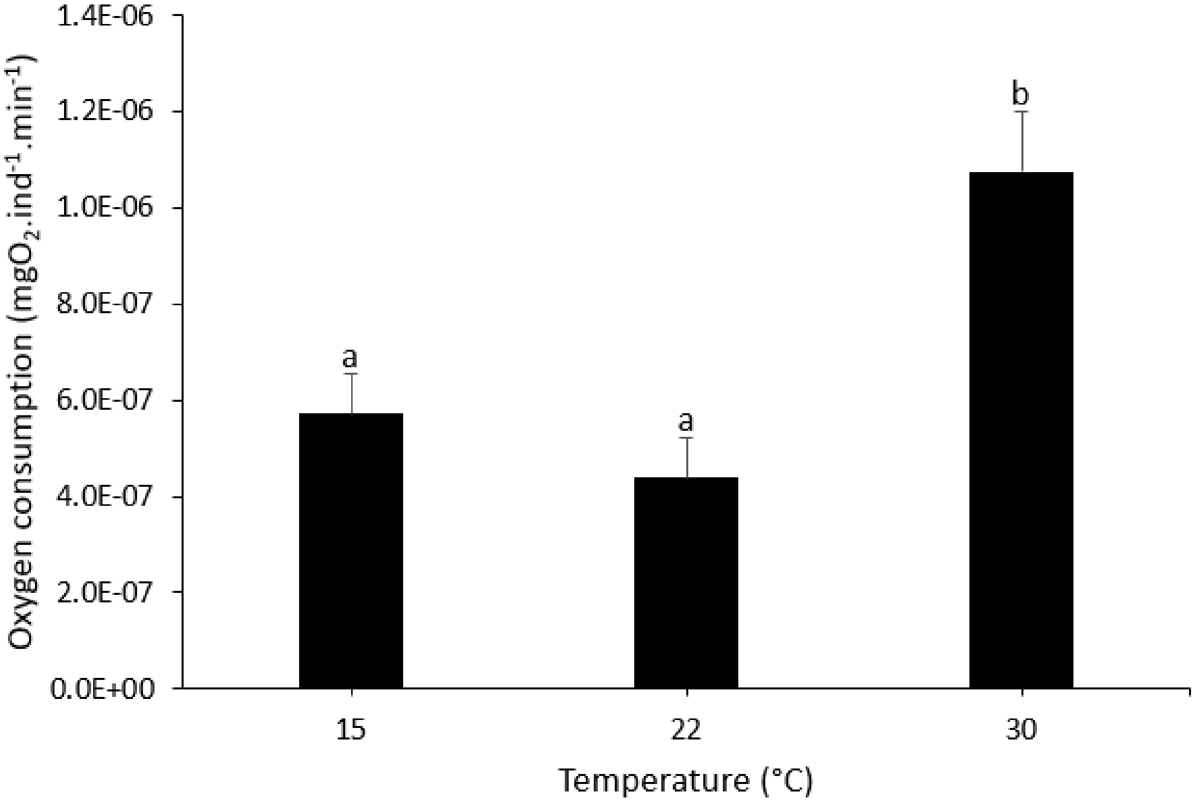

Figure 5.2: Average oxygen consumption of recruits collected at Skoenmakerskop in January 2019, tested under three different temperatures. The letters above the histogram bars indicate homogenous groups across temperatures identified by a pairwise test performed on the effect of temperature. Error bars indicate standard errors.

Chelsea Point (CP)

There was a significant effect of temperature on the oxygen consumption of recruits in February (Table 5.3) and March 2019 (Table 5.4). In both these months, oxygen consumptions were statistically higher at average and maximum than minimum temperatures (Figures 5.3 and 5.4).

Table 5.3: A 1-way permanova examining the effects of temperature on the oxygen consumption of recruits collected at Chelsea Point in February 2019. Degrees of freedom (df); Sum of Squares (SS); Mean Squares (MS); pseudo-F-ratio (Pseudo-F); permutational p-value [P(perm)] are shown; number of permutations (Unique perms); and p-value of Monte Carlo test [P(MC)] are shown.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Temperature	2	14382	7190.8	7.8609	0.001	997	0.001
Residual	53	48482	914.76				
Total	55	62864					

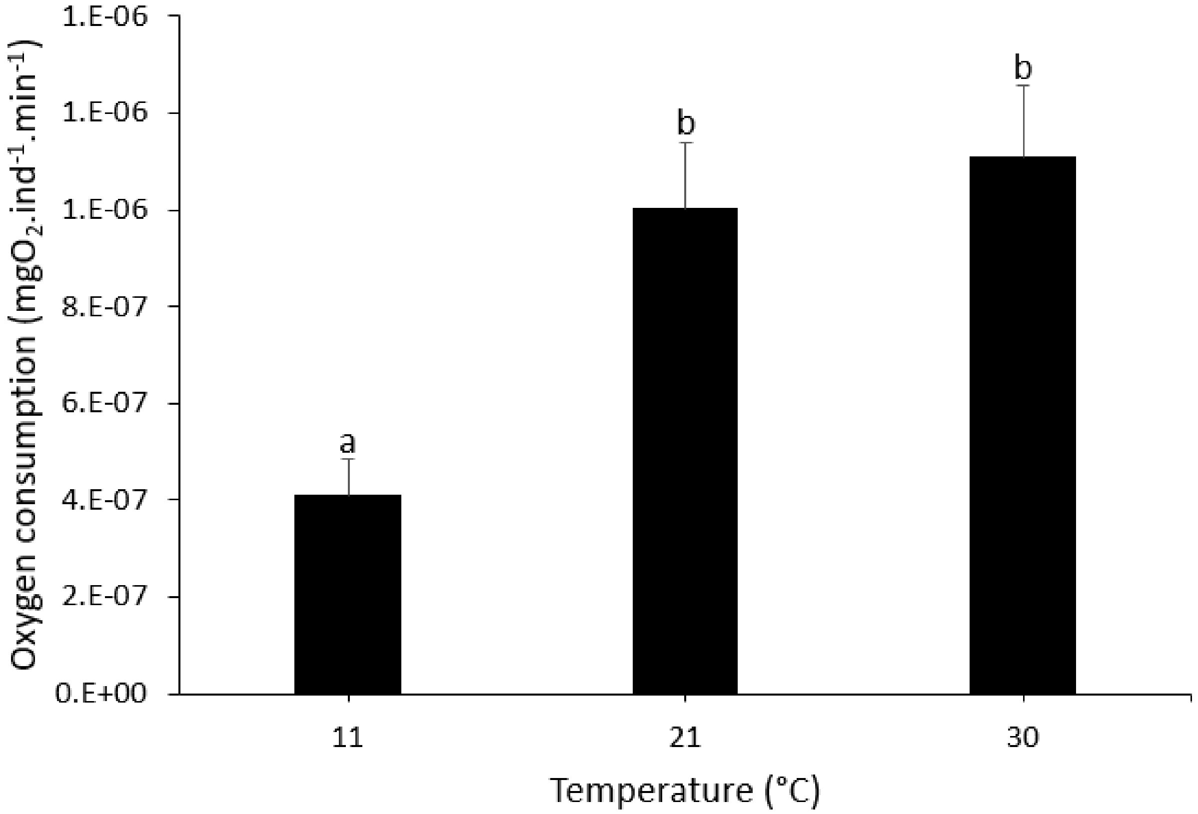

Figure 5.3: Average oxygen consumption of recruits collected at Chelsea Point in February 2019, tested under three different temperatures. The letters above the histogram bars indicate homogenous groups across temperatures identified by a pairwise test performed on the effect of temperature. Error bars indicate standard errors.

Table 5.4: A 1-way permanova examining the effects of temperature on the oxygen consumption of recruits collected at Chelsea Point in March 2019. Degrees of freedom (df); Sum of Squares (SS); Mean Squares (MS); pseudo-F-ratio (Pseudo-F); permutational p-value [P(perm)] are shown; number of permutations (Unique perms); and p-value of Monte Carlo test [P(MC)] are shown.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Temperature	2	15686	7843	7.0268	0.001	999	0.001
Residual	51	56924	1116.2				
Total	53	72610					

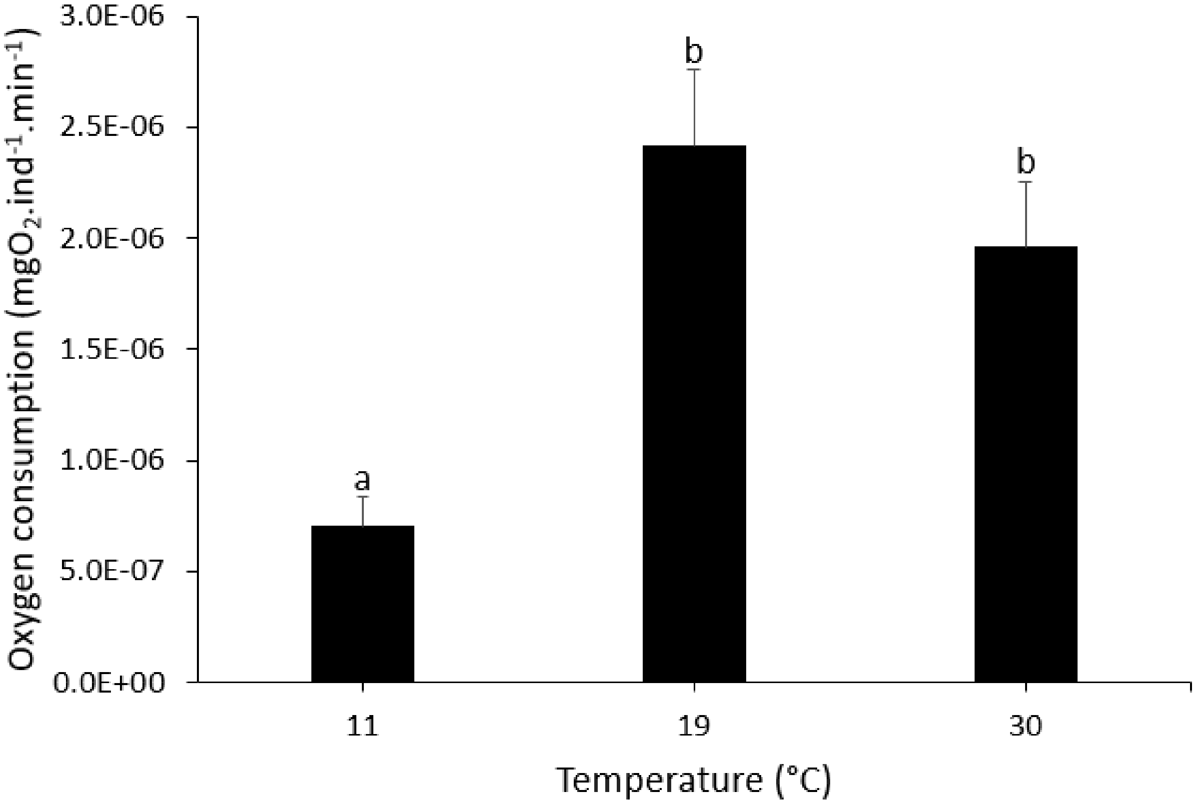

Figure 5.4: Average oxygen consumption of recruits collected at Chelsea Point in March 2019, tested under three different temperatures. The letters above the histogram bars indicate homogenous groups across temperatures identified by a pairwise test performed on the effect of temperature. Error bars indicate standard errors.

Boardwalk (BDW)

There were significant effects of temperature on the oxygen consumption of recruits in January (Table 5.5), February (Table 5.6), and March 2019 (Table 5.7). In January 2019, the average oxygen consumed was statistically the highest at the maximum temperature (Figure 5.5), while the statistically higher average oxygen consumed in February 2019 was at the mean and maximum temperatures (Figure 5.6). In March 2019, the highest oxygen consumption rate was at the average temperature, followed by the maximum temperature with the lowest consumption at the lowest temperature (Figure 5.7).

Table 5.5: A 1-way permanova examining the effects of temperature on the oxygen consumption of recruits collected at Boardwalk in January 2019. Degrees of freedom (df); Sum of Squares (SS); Mean Squares (MS); pseudo-F-ratio (Pseudo-F); permutational p-value [P(perm)] are shown; number of permutations (Unique perms); and p-value of Monte Carlo test [P(MC)] are shown.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Temperature	1	6957.4	6957.4	12.938	0.001	997	0.003
Residual	34	18284	537.76				
Total	35	25241					

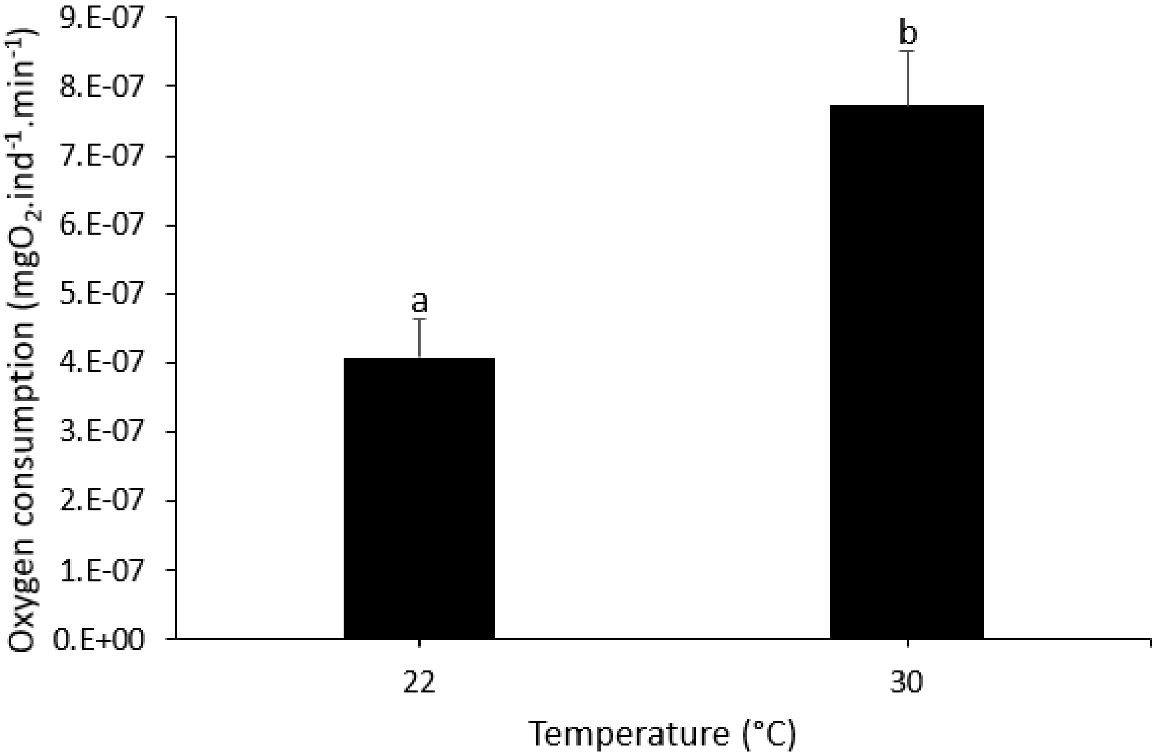

Figure 5.5: Average oxygen consumption of recruits collected at Boardwalk in January 2019, tested under two different temperatures. The letters above the histogram bars indicate homogenous groups across temperatures identified by a pairwise test performed on the effect of temperature. Error bars indicate standard errors.

Table 5.6: A 1-way permanova examining the effects of temperature on the oxygen consumption of recruits collected at Boardwalk in February 2019. Degrees of freedom (df); Sum of Squares (SS); Mean Squares (MS); pseudo-F-ratio (Pseudo-F); permutational p-value [P(perm)] are shown; number of permutations (Unique perms); and p-value of Monte Carlo test [P(MC)] are shown.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Temperature	2	8218.4	4109.2	4.7293	0.005	998	0.003
Residual	112	97315	868.88				
Total	114	1.06E+05					

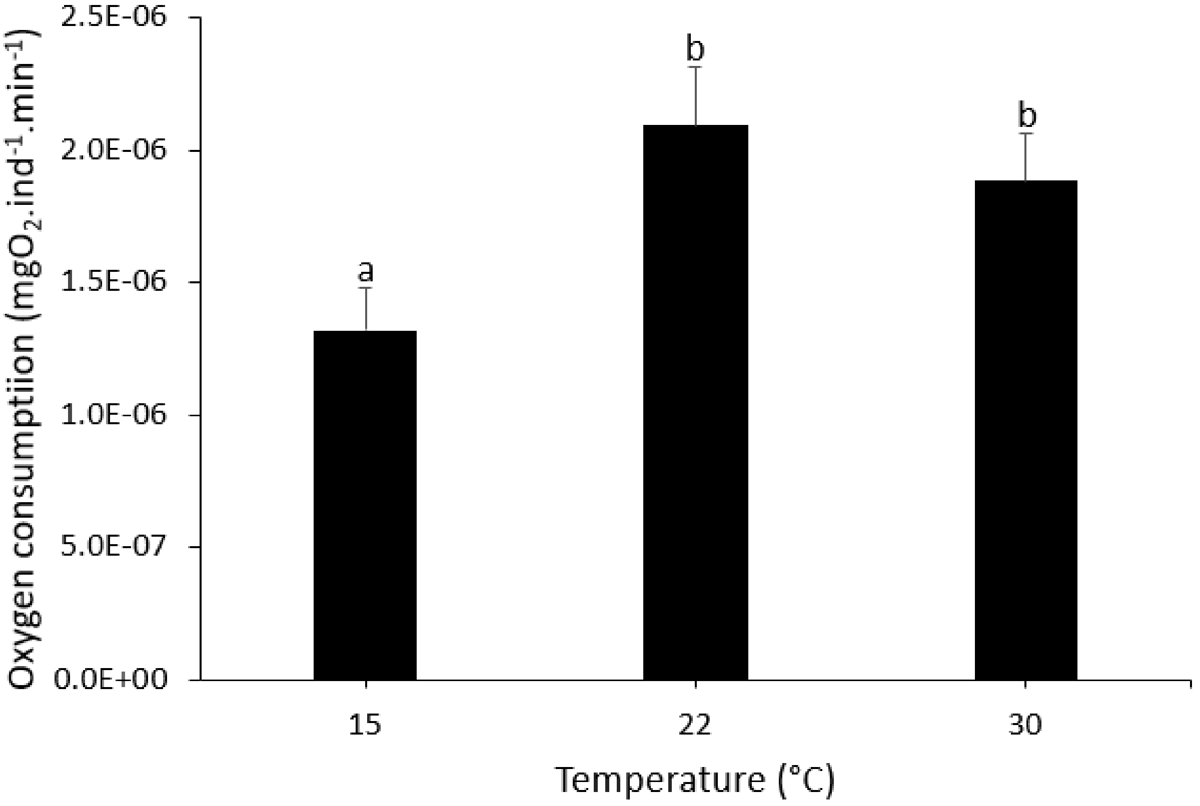

Figure 5.6: Average oxygen consumption of recruits collected at Boardwalk in February 2019, tested under three different temperatures. The letters above the histogram bars indicate homogenous groups across temperatures identified by a pairwise test performed on the effect of temperature. Error bars indicate standard errors.

Table 5.7: A 1-way permanova examining the effects of temperature on the oxygen consumption of recruits collected at Boardwalk in March 2019. Degrees of freedom (df); Sum of Squares (SS); Mean Squares (MS); pseudo-F-ratio (Pseudo-F); permutational p-value [P(perm)] are shown; number of permutations (Unique perms); and p-value of Monte Carlo test [P(MC)] are shown.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Temperature	2	19775	9887.4	6.981	0.001	999	0.001
Residual	43	60902	1416.3				
Total	45	80677					

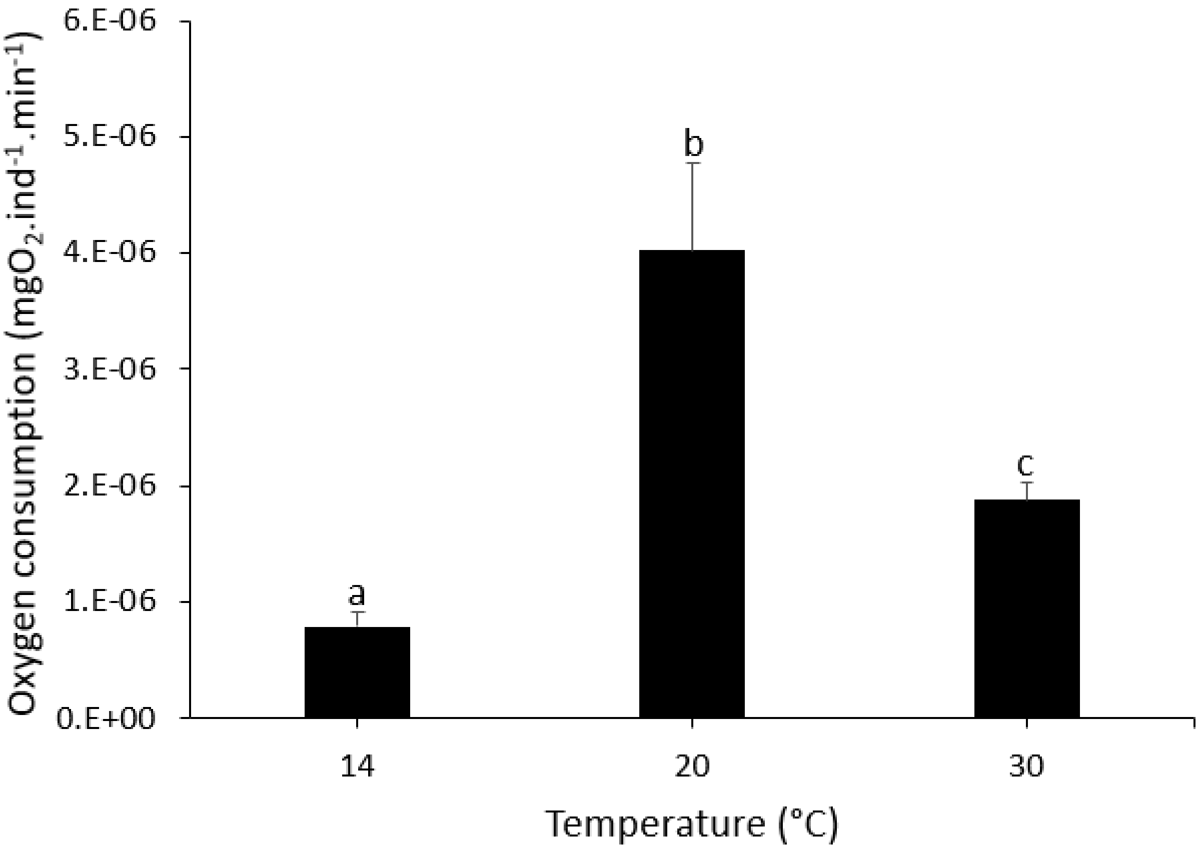

Figure 5.7: Average oxygen consumption of recruits collected at Boardwalk in March 2019, tested under three different temperatures. The letters above the histogram bars indicate homogenous groups across temperatures identified by a pairwise test performed on the effect of temperature. Error bars indicate standard errors.

Brighton Beach (BB)

There was a significant effect of temperature on the oxygen consumption of recruits in April 2019 (Table 5.8), indicating that a temperature change resulted in a change in oxygen consumption. A statistically higher average oxygen consumption was noted at average and maximum temperatures (Figure 5.8).

Table 5.8: A 1-way permanova examining the effects of temperature on the oxygen consumption of recruits collected at Brighton Beach in April 2019. Degrees of freedom (df); Sum of Squares (SS); Mean Squares (MS); pseudo-F-ratio (Pseudo-F); permutational p-value [P(perm)] are shown; number of permutations (Unique perms); and p-value of Monte Carlo test [P(MC)] are shown.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Temperature	2	15192	7595.9	7.4218	0.003	999	0.001
Residual	51	52197	1023.5				
Total	53	67389					

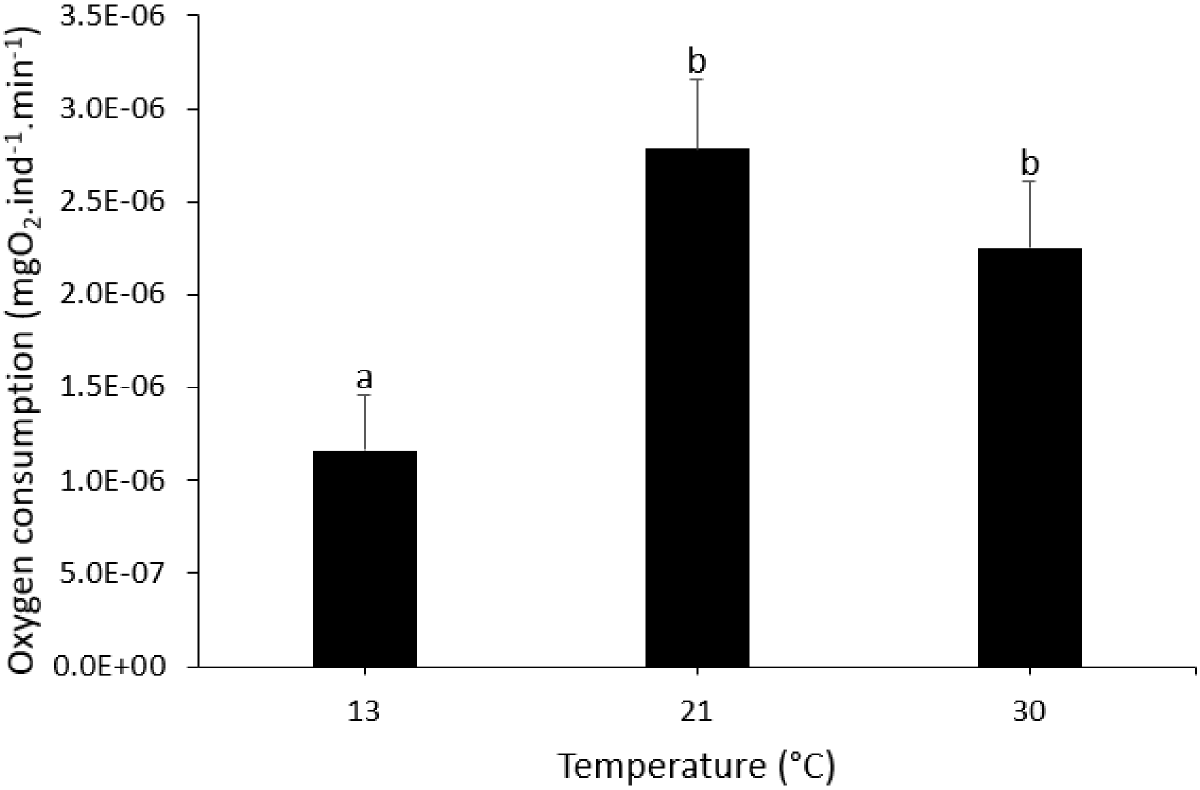

Figure 5.8: Average oxygen consumption of recruits collected at Brighton Beach in April 2019, tested under three different temperatures. The letters above the histogram bars indicate homogenous groups across temperatures identified by a pairwise test performed on the effect of temperature. Error bars indicate standard errors.

5.4. Discussion

Unlike other species with a biphasic life cycle such as decapods (Vorsatz *et al.*, 2021) and bivalves (Sprung 1984), in this study we did not note a metabolic response to temperature changes with ontogeny (in this case from settler to recruit), although this could be tested only for one month. The stage of biphasic organisms that is physiologically most sensitive (Pandori & Sorte, 2019) and energy demanding (Widdows, 1991) is the larval stage rather than the juvenile and adult stages (Foster 1969; Pandori & Sorte, 2019). Larval growth (Widdows, 1991) and metamorphosis, for example, are energy demanding, and larvae undergoing these processes show elevated metabolic rates (García-Esquivel *et al.*, 2001) and are likely to consume more oxygen than the later stages of development. This is because the larval growth rate needs to be maximised so as to have a shorter time in the plankton and reduce the chances of mortality (Widdows, 1991). At the post-settlement phase (settler and recruit), development is complete (Widdows, 1991) and the organisms become sedentary, and need less energy as they almost stop moving altogether (Limbourn *et al.*, 2008). The metabolism of settlers and recruits was not different, as both stages had passed the crucial metamorphosis period and occupied the same intertidal habitat, and therefore were likely to experience similar environmental conditions.

Over the short-term respirometry experiments, mussel recruits at different sites over different months, with different thermal histories, showed that respiration at low temperatures was reduced (lowest tested per experimental trial, which was during high tide submersion), with mostly no difference at average and raised temperatures (Figures 5.2–5.8). The oxygen consumption of mussel recruits showed a coarsely correlated relationship with temperature (from lowest testing to the average testing temperature maximum), with an increase in oxygen consumption at increasing temperatures, but not between average and maximum temperatures, as there was no statistical difference observed. This coarse relationship should be explained with caution as the full range of such correlation or relationship can only be fully assessed by testing more than three temperatures. This result shown by the early life stage, recruits, has also been observed in mussel larvae (Vihtakari *et al.*, 2013) and adult mussels from temperate regions (Thyrring *et al.*, 2015). Adult stages of *Perna perna* (the eastern lineage) and *Mytilus galloprovincialis* in South Africa showed limited oxygen consumption when tested under water at a low temperature of 18°C, compared to a temperature of 27°C (Tagliarolo & McQuaid, 2015). This pervasive pattern, observed in adults (Tagliarolo & McQuaid, 2015) and in the early stages (in this study), is indicative that these mussel species actively consume more oxygen at higher temperatures than in cooler temperatures (Bruce, 1926; Fly *et al.*, 2015). In other temperate regions, respiration rates of adults of the mussel species *Modiolus modiolus* have also been generally higher in summer than in winter (Lesser & Kruse, 2004), suggesting that there is a correlation between mussel respiration and temperature. As dissolved oxygen concentrations decrease with an increase in water temperature (Fang & Stefan, 2009), organisms may increase their respiration rate (Jansen *et al.*, 2009) or increase the amount of water processed to compensate for the limited oxygen concentration in the water. In this study however, filtration rates were not measured. This study concurs with the results of studies on adult *Pinna nobilis* and the genus *Mytilus*, which both showed an increase in their respiration rates at elevated temperatures (Zippay & Helmuth, 2012; Trigos *et al.*, 2015).

Low temperatures result in low metabolic rates and therefore lower demand of ATP, (Lesser & Kruse, 2004), suggesting the opposite should occur with increased temperatures. Organisms use different strategies to deal with extreme temperatures (Lesser & Kruse, 2004). Firstly, organisms employ behavioural mechanisms, then metabolic adjustments, and lastly heat-shock protein (hsp) expression (Anestis *et al.*, 2007). As a behavioural mechanism, some bivalves increase or decrease the frequency and duration of valve closure and opening

(Anestis *et al*., 2007). Increased duration of valve closure induces tissue hypoxia (Ortmann & Grieshaber, 2003), and therefore bivalves move to the second phase, through metabolic adjustments, which involves changing from aerobic to anaerobic respiration (Anestis *et al*., 2007; 2008). Anaerobiosis leads to metabolic depression and denaturing of other proteins (Storey & Storey, 1990; Brooks & Storey, 1997; Ortmann & Grieshaber, 2003) and subsequently the final step is to employ heat-shock proteins (Hofmann & Somero, 1995; Anestis *et al*., 2007; 2008; Lesser, 2016). These heat shock proteins are important in cellular protection against environmental stress (Mićović *et al*., 2009), specifically temperature (Castelli *et al*., 2004; Dahlhoff, 2004), as they assist in re-folding other thermally denatured proteins (Hofmann & Somero, 1995; Feder & Hofmann, 1999). The re-folding of thermally damaged proteins is a behaviour used to revive denatured enzymes (proteins) that are responsible for metabolism at elevated temperatures (Hofmann, 2005).

Thermal responses of juveniles could be comparable to conspecific adult mussels. Though they differ in their surface: volume ratio, adults and juveniles live in the same intertidal zone, are exposed to similar physical factors such as tidal exposure and submersion, and are similar in behaviours such as opening and closing of the valves (Trevelyan & Chang, 2009). This is however, increasingly debatable as mussel settlers and/or recruits (Gleason *et al*., 2018) and juvenile barnacles (Lathlean *et al*., 2013) are mostly found in microhabitats (interstitial spaces within adult beds) that are relatively moist and sheltered from exposure to direct sunlight by adults (Lathlean *et al*., 2013; Gleason *et al*., 2018). Rock temperatures decrease with increasing proximity to conspecific adult populations (Lathlean *et al*., 2013) and microhabitat choice by settling individuals is partly said to be triggered by thermal stress (Moisez *et al*., 2020). That means that competent larvae actively prefer settling within spatially complex areas or interstitial spaces rather than as solitary individuals (Wethey, 1986). Mussels living as solitary individuals tend to have increased body temperatures compared to aggregated mussels (Helmuth, 1998), suggesting that temperature is lower within mussel beds, and therefore settlers and recruits experience cooler temperatures in the interstitial spaces of mussel beds. Spatial complexity in mussel beds, therefore, not only provides refuge from predators (Bertolini *et al.*, 2018), but also mitigates environmental conditions (Lourenço *et al.*, 2017) such as wave force (O'Donnell, 2008), water flow (van Leeuwen *et al.*, 2010) and thermal stress (Stephens & Bertness, 1991).

It is noteworthy, however, that at BDW, in March 2019, there was a statistically significant decline in oxygen uptake from the average temperature of 20°C to the maximum temperature of 30°C, although the statistically lowest oxygen uptake was at the lowest testing temperature of 14°C (Figure 5.7). Environmental temperature has an impact on protein activity (involving dormancy at low temperatures and denaturing at high temperatures; Hofmann & Somero, 1995; 1996) and this, therefore affects the metabolism of organisms (Sokolova & Lannig, 2008) through enhanced/reduced/collapsed cellular respiration. The decrease in oxygen consumption at the maximum temperature could have been a result of denaturing of enzymes and therefore slower/collapsed metabolism. It should also be noted that anaerobic metabolism does set in at both cold and hot temperatures (Anestis *et al.*, 2007). This might be the reason for the low oxygen uptake in the lowest and highest temperatures in March 2019 at BDW, particularly given the fact that the maximum temperature experienced in the field was 26°C and the maximum testing temperature was 30°C, and the animals may have not coped with this temperature difference (which was larger than for any other site/month combinations).

While the aim of the study was to test whether the thermal exposure of competent mussel larvae during settlement would affect the thermal sensitivity of settlers and/or recruits, the results did not support my hypothesis. Organisms collected at an average high temperature did not differ in oxygen consumption from those collected at an average lower temperature, as both stages showed limited oxygen consumption at the lowest testing temperature and increased consumption at average and maximum temperatures. The thermal history of recruits therefore did not affect their thermal plasticity and sensitivity to temperature changes, as all recruits showed an ability to tolerate all the temperatures at which they were tested.

In conclusion, during the larval-juvenile-adult transition, certain physiological plasticity is key, as organisms are likely to face severe changes and highly variable temperature regimes, from very cold to extremely hot in a short period of time. Quick adaptation to this stressful environment (in the intertidal zone) is a matter of life and death, with no exception for early life stages. However, settlers and recruits living in this zone are sometimes assisted by their conspecifics in terms of providing a microhabitat whereby environmental events such as temperature extremes are buffered by the adults.

Chapter 6

General Discussion

This study aimed to investigate the effects of wind on spatial and temporal variation in marine invertebrate dispersal and settlement along the south east coast of South Africa. With the majority of marine benthic species having a biphasic life cycle, and larvae developing in the water column before settling on the rocky shores, it was also important to understand the physiological implications for settling organisms as they were affected by physical environmental conditions prior to settlement.

Wind played a role in the nearshore ocean circulation (Figures 2.2–2.8), thereby affecting the distribution and transport of invertebrate larvae. The dissipation of turbulent kinetic energy, together with zonal flow, for example, are largely determined by wind speed and direction (Tanaka, 2019). Together, these oceanic processes explained up to 32% and 13% of the abundance of anomuran and brachyuran zoeae, respectively (Table 2.8). An increase in wind speed amplifies water surface dissipation of turbulent kinetic energy, which plays a role in the distribution of larvae in the water column, as some species prefer calmer waters (Fuchs *et al.*, 2007). The abundance of larvae in this study related negatively to the dissipation of turbulent kinetic energy, and this resulted in increased abundances at the mid- and bottom depths. This bottom distribution of larvae would also increase their chances of onshore advection during an upwelling event.

During the period between September 2017 and March 2018 (summer), a spike in frequency and speed of easterly winds was noticed (Figures 3.2–3.5). In this region, easterly winds are known to result in upwelling events (Schumann & Martin, 1991). The increase in wind speed (and associated increase in the dissipation of turbulent kinetic energy) from the east (resulting in upwelling) could have resulted in larvae sinking to the bottom as a dissipation of turbulent kinetic energy avoidance strategy, and being swept onshore with upwelling waters. The net effect of this would be an increase in settlement and/or recruitment of organisms.

The abundance of *Perna perna* settlers and recruits increased between February and June 2018 (Figures 3.6 and 3.7 respectively), which coincided with the last month of increased easterly wind frequency and therefore of an upwelling event. Settlement and recruitment of the invasive *Mytilus galloprovincialis* on the other hand, increased between October 2017 and February 2018 (Figures 3.8 and 3.9 respectively). Mytilid species that share characteristics such as the pelagic larval duration (Carson *et al.*, 2010), tend to settle around the same time if they reproduce at the same time. The temporal unmatching in settlement and/or recruitment between the two species might therefore be a result of differences in spawning times (Zardi *et al.*, 2007). Settlement of barnacles on the other hand, increased between January and May 2018 (Figure 3.12). These periods of increased settlement of mussels and barnacles were either well within the upwelling events, suggesting that upwelling might have played a role in transporting larvae and delivering them to the shore. This mechanism is possible, as larvae which inhabit layers of water below the thermocline are likely to be advected shoreward during upwelling (Shanks & Brink, 2005). Shoreward advection of larvae by upwelling waters has indeed been shown (Pineda, 1991), and, although settlement may not reflect the larval pool, larval supply and delivery to the shore are important determinants of settlement intensity (Pineda *et al.*, 2010). It has also been suggested that a series of mechanisms are necessary for larval supply and successful settlement on the rocky shores (Pfaff *et al.*, 2015).

Upwelling brings cold, nutrient rich bottom water to the surface of the water column (Kämpf & Chapman, 2016). These nutrient-rich waters increase the feeding opportunities of filter feeders that have settled on the shore. However, organisms are then faced with cold water, from the time they are transported shoreward and during upwelling, as they have already settled on the rocky shores. During low tide, those settled organisms are now faced with different environmental conditions (thermal, and others) to those they experienced as larvae in the water column.

Transport to the shore in cold, upwelling waters and then facing the shock of high temperatures on the rocks during the summer low tides require organisms to adapt quickly or die. Recruits found on the rocky shores showed sensitivity to extreme temperature events, with a decline in respiration at low temperatures and an increase at high temperatures. This physiological plasticity might either assist recruits to survive the unpredictable and highly variable environment posed by the intertidal zone or indicate the top end of physiological performance (*sensu pejus* condition, Pörtner 2001).

In conclusion, wind indirectly played a role in larval distribution and transport. Wind speed and direction played a direct role in nearshore ocean hydrodynamics. These hydrodynamic factors were directly responsible for the distribution of larvae at certain depths of the water column (Fuchs *et al*., 2010; 2015), which later enabled larvae to be transported and supplied to the shore through processes including upwelling. Physiological mechanisms may have reduced the survival of settlers, especially during an upwelling event, as the organisms would have been delivered with upwelling cold water (Marta-Almeida *et al*., 2006) and some barnacle cyprids would use their lipid reserves in cold waters (Holland & Walker, 1975) and would have then been faced early in their life with extremely high temperatures during low tide (through exposure to direct sunlight).

Wind and wind-driven currents can therefore be concluded to be among main drivers of larval distribution and delivery to the shore. Thereafter, temperature might play a key role in the survival of settled organisms. Overall, together these physical factors play a direct role in the early shaping of population dynamics of benthic intertidal organisms.

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Appendices

Chapter 2

Table A1: Benjamini-Hochberg correction for the ANOVA analyses on all the taxa analysed. (*i/m*)**Q* = Benjamini-Hochberg critical value where *i* = Rank, *m* = total number of tests, and Q = false discovery rate of 0.05. The bold row shows the cut-off point of significance.

p	*Rank*	*B-H*
0,000	1	0,001
0,000	2	0,001
0,000	3	0,002
0,000	4	0,003
0,000	5	0,003
0,000	6	0,004
0,001	7	0,005
0,001	8	0,005
0,004	9	0,006
0,006	**10**	**0,007**
0,008	11	0,007
0,009	12	0,008
0,015	13	0,009
0,019	14	0,009
0,019	15	0,010
0,023	16	0,011
0,027	17	0,011
0,027	18	0,012
0,032	19	0,013
0,033	20	0,013
0,034	21	0,014
0,049	22	0,015
0,053	23	0,015
0,054	24	0,016
0,083	25	0,017
0,091	26	0,017
0,108	27	0,018
0,120	28	0,019
0,148	29	0,019
0,190	30	0,020
0,214	31	0,021
0,217	32	0,021
0,219	33	0,022
0,242	34	0,023
0,272	35	0,023
0,286	36	0,024
0,289	37	0,025
0,301	38	0,025
0,301	39	0,026
0,305	40	0,027
0,397	41	0,027
0,400	42	0,028
0,528	43	0,029
0,532	44	0,029
0,550	45	0,030
0,574	46	0,031
0,575	47	0,031
0,631	48	0,032
0,645	49	0,033
0,652	50	0,033
0,691	51	0,034
0,696	52	0,035
0,710	53	0,035
0,722	54	0,036
0,752	55	0,037
0,756	56	0,037
0,757	57	0,038
0,793	58	0,039
0,796	59	0,039
0,804	60	0,040
0,812	61	0,041
0,813	62	0,041
0,844	63	0,042
0,847	64	0,043
0,870	65	0,043
0,889	66	0,044
0,905	67	0,045
0,921	68	0,045
0,923	69	0,046
0,946	70	0,047
0,952	71	0,047
0,962	72	0,048
0,972	73	0,049
0,984	74	0,049
0,995	75	0,050

Table A2: Benjamini-Hochberg correction for the multiple regression analyses on all the taxa analysed. (*i/m*)**Q* = Benjamini-Hochberg critical value where *i* = Rank, *m* = total number of tests, and Q = false discovery rate of 0.05. The bold row shows the cut-off point of significance.

p	*Rank*	*B-H*
<0,001	1	0,000
<0,001	2	0,000
<0,001	3	0,001
<0,001	4	0,001
<0,001	5	0,001
<0,001	6	0,001
<0,001	7	0,001
<0,001	8	0,002
<0,001	9	0,002
<0,001	10	0,002
<0,001	11	0,002
<0,001	12	0,003
<0,001	13	0,003
<0,001	14	0,003
<0,001	15	0,003
<0,001	16	0,003
<0,001	17	0,004
<0,001	18	0,004
<0,001	19	0,004
<0,001	20	0,004
<0,001	21	0,004
<0,001	22	0,005
<0,001	23	0,005
<0,001	24	0,005
<0,001	25	0,005
<0,001	26	0,005
<0,001	27	0,006
<0,001	28	0,006
<0,001	29	0,006
<0,001	30	0,006
<0,001	31	0,006
<0,001	32	0,007
<0,001	33	0,007
<0,001	34	0,007
<0,001	35	0,007
<0,001	36	0,008
<0,001	37	0,008
<0,001	38	0,008
<0,001	39	0,008
<0,001	40	0,008
<0,001	41	0,009
<0,001	42	0,009
<0,001	43	0,009
<0,001	44	0,009
<0,001	45	0,009
<0,001	46	0,010
<0,001	47	0,010
<0,001	48	0,010
<0,001	49	0,010
<0,001	50	0,010
<0,001	51	0,011
<0,001	52	0,011
<0,001	53	0,011
<0,001	54	0,011
<0,001	55	0,011
<0,001	56	0,012
<0,001	57	0,012
<0,001	58	0,012
<0,001	59	0,012
<0,001	60	0,013
<0,001	61	0,013
<0,001	62	0,013
<0,001	63	0,013
<0,001	64	0,013
<0,001	65	0,014
<0,001	66	0,014
<0,001	67	0,014
<0,001	68	0,014
<0,001	69	0,014
<0,001	70	0,015
<0,001	71	0,015
<0,001	72	0,015
<0,001	73	0,015
<0,001	74	0,015
<0,001	75	0,016
<0,001	76	0,016
<0,001	77	0,016
<0,001	78	0,016
<0,001	79	0,016
<0,001	80	0,017
<0,001	81	0,017
<0,001	82	0,017
<0,001	83	0,017
<0,001	84	0,018
<0,001	85	0,018
<0,001	86	0,018
<0,001	87	0,018
<0,001	88	0,018
<0,001	89	0,019
<0,001	90	0,019
<0,001	91	0,019
<0,001	92	0,019
<0,001	93	0,019
<0,001	94	0,020
<0,001	95	0,020
<0,001	96	0,020
<0,001	97	0,020
<0,001	98	0,020
<0,001	99	0,021
<0,001	100	0,021
<0,001	101	0,021
0,001	102	0,021
0,001	103	0,021
0,001	104	0,022
0,001	105	0,022
0,001	106	0,022
0,001	107	0,022
0,001	108	0,023
0,002	109	0,023
0,002	110	0,023
0,002	111	0,023
0,002	112	0,023
0,002	113	0,024
0,002	114	0,024
0,002	115	0,024
0,003	116	0,024
0,003	117	0,024
0,003	118	0,025
0,003	119	0,025
0,003	120	0,025
0,004	121	0,025
0,004	122	0,025
0,004	123	0,026
0,004	124	0,026
0,004	125	0,026
0,004	126	0,026

p	*Rank*	*B-H*
0,005	127	0,026
0,005	128	0,027
0,005	129	0,027
0,005	130	0,027
0,006	131	0,027
0,006	132	0,028
0,006	133	0,028
0,006	134	0,028
0,007	135	0,028
0,008	136	0,028
0,008	137	0,029
0,01	138	0,029
0,011	139	0,029
0,012	140	0,029
0,013	141	0,029
0,013	142	0,030
0,014	143	0,030
0,016	144	0,030
0,019	145	0,030
0,021	146	0,030
0,021	147	0,031
0,022	148	0,031
0,024	149	0,031
0,024	150	0,031
0,026	151	**0,031**
0,033	152	0,032
0,036	153	0,032
0,037	154	0,032
0,039	155	0,032
0,04	156	0,033
0,04	157	0,033
0,044	158	0,033
0,045	159	0,033
0,047	160	0,033
0,051	161	0,034
0,053	162	0,034
0,062	163	0,034
0,071	164	0,034
0,072	165	0,034
0,073	166	0,035
0,075	167	0,035
0,077	168	0,035
0,081	169	0,035
0,092	170	0,035
0,105	171	0,036
0,144	172	0,036
0,148	173	0,036
0,151	174	0,036
0,161	175	0,036
0,166	176	0,037
0,173	177	0,037
0,195	178	0,037
0,195	179	0,037
0,202	180	0,038
0,206	181	0,038
0,241	182	0,038
0,271	183	0,038
0,284	184	0,038
0,291	185	0,039
0,293	186	0,039
0,294	187	0,039
0,315	188	0,039
0,336	189	0,039
0,342	190	0,040
0,361	191	0,040
0,37	192	0,040
0,38	193	0,040
0,386	194	0,040
0,398	195	0,041
0,407	196	0,041
0,417	197	0,041
0,434	198	0,041
0,45	199	0,041
0,487	200	0,042
0,493	201	0,042
0,499	202	0,042
0,516	203	0,042
0,531	204	0,043
0,54	205	0,043
0,541	206	0,043
0,543	207	0,043
0,544	208	0,043
0,555	209	0,044
0,579	210	0,044
0,579	211	0,044
0,595	212	0,044
0,609	213	0,044
0,642	214	0,045
0,651	215	0,045
0,672	216	0,045
0,674	217	0,045
0,71	218	0,045
0,716	219	0,046
0,72	220	0,046
0,759	221	0,046
0,771	222	0,046
0,781	223	0,046
0,786	224	0,047
0,807	225	0,047
0,818	226	0,047
0,826	227	0,047
0,827	228	0,048
0,85	229	0,048
0,858	230	0,048
0,869	231	0,048
0,884	232	0,048
0,889	233	0,049
0,891	234	0,049
0,901	235	0,049
0,909	236	0,049
0,911	237	0,049
0,932	238	0,050
0,944	239	0,050
0,984	240	0,050

Chapter 3

Table A3: Benjamini-Hochberg correction for the ANOVA analyses on all the taxa analysed. $(i/m)*Q$ = Benjamini-Hochberg critical value where i = Rank, m = total number of tests, and Q = false discovery rate of 0.05. The bold row shows the cut-off point of significance.

p	*Rank*	*B-H*
<0.0001	1	0.0021
<0.0001	2	0.0042
<0.0001	3	0.0063
<0.0001	4	0.0083
<0.0001	5	0.0104
<0.0001	6	0.0125
<0.0001	7	0.0146
<0.0001	8	0.0167
<0.0001	9	0.0188
<0.0001	10	0.0208
<0.0001	11	0.0229
<0.0001	12	0.0250
<0.0001	13	0.0271
<0.0001	14	0.0292
<0.0001	15	0.0313
<0.0001	16	0.0333
<0.0001	17	0.0354
<0.0001	18	0.0375
<0.0001	19	0.0396
<0.0001	20	0.0417
<0.0001	21	0.0438
<0.0001	22	0.0458
<0.0001	23	0.0479
<0.0001	24	0.0500

Table A4: Benjamini-Hochberg correction for the multiple regression analyses on all the taxa analysed. (*i/m*)**Q* = Benjamini-Hochberg critical value where *i* = Rank, *m* = total number of tests, and Q = false discovery rate of 0.05. The bold row shows the cut-off point of significance.

p	*Rank*	*B-H*
<0.001	1	0,000
<0.001	2	0,000
<0.001	3	0,000
<0.001	4	0,000
<0.001	5	0,001
0.001	**6**	**0,001**
0.002	7	0,001
0.002	8	0,001
0.003	9	0,001
0.003	10	0,001
0.004	11	0,001
0.007	12	0,001
0.008	13	0,002
0.008	14	0,002
0.009	15	0,002
0.009	16	0,002
0.011	17	0,002
0.012	18	0,002
0.013	19	0,002
0.016	20	0,002
0.017	21	0,003
0.019	22	0,003
0.019	23	0,003
0.019	24	0,003
0.021	25	0,003
0.022	26	0,003
0.024	27	0,003
0.026	28	0,003
0.027	29	0,003
0.029	30	0,004
0.035	31	0,004
0.041	32	0,004
0.041	33	0,004
0.042	34	0,004
0.048	35	0,004
0.05	36	0,004
0.054	37	0,004
0.056	38	0,005
0.061	39	0,005
0.069	40	0,005
0.073	41	0,005
0.076	42	0,005
0.078	43	0,005
0.081	44	0,005
0.083	45	0,005
0.089	46	0,005
0.09	47	0,006
0.091	48	0,006
0.093	49	0,006
0.096	50	0,006
0.102	51	0,006
0.102	52	0,006
0.104	53	0,006
0.106	54	0,006
0.111	55	0,007
0.116	56	0,007
0.117	57	0,007
0.117	58	0,007
0.121	59	0,007
0.122	60	0,007
0.124	61	0,007
0.126	62	0,007
0.126	63	0,008
0.132	64	0,008
0.133	65	0,008
0.134	66	0,008
0.135	67	0,008
0.142	68	0,008
0.144	69	0,008
0.149	70	0,008
0.153	71	0,008
0.153	72	0,009
0.154	73	0,009
0.163	74	0,009
0.164	75	0,009
0.165	76	0,009
0.171	77	0,009
0.171	78	0,009
0.174	79	0,009
0.177	80	0,010
0.177	81	0,010
0.181	82	0,010
0.182	83	0,010
0.182	84	0,010
0.185	85	0,010
0.192	86	0,010
0.192	87	0,010
0.195	88	0,010
0.197	89	0,011
0.197	90	0,011
0.198	91	0,011
0.198	92	0,011
0.204	93	0,011
0.207	94	0,011
0.209	95	0,011
0.211	96	0,011
0.217	97	0,012
0.22	98	0,012
0.22	99	0,012
0.22	100	0,012
0.221	101	0,012
0.222	102	0,012
0.225	103	0,012
0.227	104	0,012
0.236	105	0,013
0.258	106	0,013
0.259	107	0,013
0.26	108	0,013
0.261	109	0,013
0.265	110	0,013
0.269	111	0,013
0.271	112	0,013
0.275	113	0,013
0.278	114	0,014
0.279	115	0,014
0.28	116	0,014
0.282	117	0,014

p	*Rank*	*B-H*
0.286	118	0,014
0.292	119	0,014
0.294	120	0,014
0.297	121	0,014
0.301	122	0,015
0.306	123	0,015
0.312	124	0,015
0.315	125	0,015
0.316	126	0,015
0.321	127	0,015
0.321	128	0,015
0.322	129	0,015
0.325	130	0,015
0.328	131	0,016
0.33	132	0,016
0.333	133	0,016
0.337	134	0,016
0.338	135	0,016
0.34	136	0,016
0.344	137	0,016
0.348	138	0,016
0.35	139	0,017
0.355	140	0,017
0.355	141	0,017
0.356	142	0,017
0.357	143	0,017
0.357	144	0,017
0.359	145	0,017
0.362	146	0,017
0.365	147	0,018
0.365	148	0,018
0.37	149	0,018
0.372	150	0,018
0.373	151	0,018
0.378	152	0,018
0.384	153	0,018
0.384	154	0,018
0.385	155	0,018
0.39	156	0,019
0.393	157	0,019
0.394	158	0,019
0.402	159	0,019
0.408	160	0,019
0.411	161	0,019
0.412	162	0,019
0.414	163	0,019
0.415	164	0,020
0.418	165	0,020
0.421	166	0,020
0.421	167	0,020
0.424	168	0,020
0.425	169	0,020
0.426	170	0,020
0.426	171	0,020
0.427	172	0,020
0.428	173	0,021
0.429	174	0,021
0.43	175	0,021
0.437	176	0,021
0.439	177	0,021
0.442	178	0,021
0.443	179	0,021
0.445	180	0,021
0.457	181	0,022
0.459	182	0,022
0.46	183	0,022
0.46	184	0,022
0.46	185	0,022
0.466	186	0,022
0.467	187	0,022
0.468	188	0,022
0.471	189	0,023
0.474	190	0,023
0.475	191	0,023
0.477	192	0,023
0.478	193	0,023
0.479	194	0,023
0.48	195	0,023
0.482	196	0,023
0.483	197	0,023
0.486	198	0,024
0.489	199	0,024
0.489	200	0,024
0.49	201	0,024
0.49	202	0,024
0.491	203	0,024
0.492	204	0,024
0.493	205	0,024
0.493	206	0,025
0.493	207	0,025
0.495	208	0,025
0.499	209	0,025
0.501	210	0,025
0.505	211	0,025
0.508	212	0,025
0.518	213	0,025
0.521	214	0,025
0.522	215	0,026
0.524	216	0,026
0.524	217	0,026
0.527	218	0,026
0.527	219	0,026
0.529	220	0,026
0.533	221	0,026
0.535	222	0,026
0.535	223	0,027
0.541	224	0,027
0.544	225	0,027
0.546	226	0,027
0.551	227	0,027
0.551	228	0,027
0.553	229	0,027
0.555	230	0,027
0.556	231	0,028
0.557	232	0,028
0.558	233	0,028
0.559	234	0,028
0.561	235	0,028
0.563	236	0,028
0.563	237	0,028
0.566	238	0,028
0.568	239	0,028
0.571	240	0,029
0.571	241	0,029
0.571	242	0,029
0.573	243	0,029
0.574	244	0,029
0.576	245	0,029
0.577	246	0,029
0.578	247	0,029
0.579	248	0,030
0.58	249	0,030
0.584	250	0,030
0.59	251	0,030
0.59	252	0,030

p	*Rank*	*B-H*
0.595	253	0,030
0.599	254	0,030
0.6	255	0,030
0.601	256	0,030
0.601	257	0,031
0.603	258	0,031
0.606	259	0,031
0.609	260	0,031
0.621	261	0,031
0.622	262	0,031
0.626	263	0,031
0.63	264	0,031
0.63	265	0,032
0.631	266	0,032
0.634	267	0,032
0.634	268	0,032
0.641	269	0,032
0.641	270	0,032
0.645	271	0,032
0.652	272	0,032
0.653	273	0,033
0.657	274	0,033
0.657	275	0,033
0.659	276	0,033
0.667	277	0,033
0.674	278	0,033
0.674	279	0,033
0.676	280	0,033
0.678	281	0,033
0.682	282	0,034
0.683	283	0,034
0.685	284	0,034
0.685	285	0,034
0.685	286	0,034
0.691	287	0,034
0.692	288	0,034
0.693	289	0,034
0.694	290	0,035
0.698	291	0,035
0.702	292	0,035
0.704	293	0,035
0.705	294	0,035
0.711	295	0,035
0.711	296	0,035
0.712	297	0,035
0.715	298	0,035
0.718	299	0,036
0.727	300	0,036
0.729	301	0,036
0.731	302	0,036
0.734	303	0,036
0.734	304	0,036
0.737	305	0,036
0.741	306	0,036
0.742	307	0,037
0.742	308	0,037
0.743	309	0,037
0.746	310	0,037
0.747	311	0,037
0.75	312	0,037
0.75	313	0,037
0.751	314	0,037
0.753	315	0,038
0.761	316	0,038
0.765	317	0,038
0.768	318	0,038
0.771	319	0,038
0.775	320	0,038
0.776	321	0,038
0.778	322	0,038
0.78	323	0,038
0.787	324	0,039
0.793	325	0,039
0.796	326	0,039
0.797	327	0,039
0.798	328	0,039
0.799	329	0,039
0.801	330	0,039
0.802	331	0,039
0.803	332	0,040
0.804	333	0,040
0.804	334	0,040
0.807	335	0,040
0.809	336	0,040
0.817	337	0,040
0.824	338	0,040
0.828	339	0,040
0.83	340	0,040
0.83	341	0,041
0.832	342	0,041
0.834	343	0,041
0.835	344	0,041
0.836	345	0,041
0.838	346	0,041
0.841	347	0,041
0.843	348	0,041
0.847	349	0,042
0.849	350	0,042
0.849	351	0,042
0.849	352	0,042
0.854	353	0,042
0.857	354	0,042
0.861	355	0,042
0.867	356	0,042
0.868	357	0,043
0.872	358	0,043
0.872	359	0,043
0.874	360	0,043
0.875	361	0,043
0.876	362	0,043
0.877	363	0,043
0.878	364	0,043
0.878	365	0,043
0.879	366	0,044
0.881	367	0,044
0.883	368	0,044
0.886	369	0,044
0.892	370	0,044
0.892	371	0,044
0.892	372	0,044
0.9	373	0,044
0.903	374	0,045
0.903	375	0,045
0.905	376	0,045
0.908	377	0,045
0.909	378	0,045
0.912	379	0,045
0.912	380	0,045
0.913	381	0,045
0.913	382	0,045
0.914	383	0,046
0.916	384	0,046

p	*Rank*	*B-H*
0.92	385	0,046
0.921	386	0,046
0.921	387	0,046
0.922	388	0,046
0.933	389	0,046
0.936	390	0,046
0.937	391	0,047
0.938	392	0,047
0.941	393	0,047
0.942	394	0,047
0.943	395	0,047
0.945	396	0,047
0.947	397	0,047
0.947	398	0,047
0.948	399	0,048
0.951	400	0,048
0.951	401	0,048
0.958	402	0,048
0.959	403	0,048
0.961	404	0,048
0.961	405	0,048
0.962	406	0,048
0.964	407	0,048
0.966	408	0,049
0.97	409	0,049
0.978	410	0,049
0.982	411	0,049
0.982	412	0,049
0.983	413	0,049
0.985	414	0,049
0.991	415	0,049
0.992	416	0,050
0.992	417	0,050
0.992	418	0,050
0.994	419	0,050
0.998	420	0,050

Table A5: Benjamini-Hochberg calculation for the correlation analyses on all the taxa analysed. (*i*/*m*)**Q* = Benjamini-Hochberg critical value where *i* = Rank, *m* = total number of tests, and Q = false discovery rate of 0.05. The bold row shows the cut-off point of significance.

p	*Rank*	*B-H*
<0.001	1	0,000
<0.001	2	0,000
<0.001	3	0,000
0.001	4	0,000
0.001	**5**	**0,001**
0.003	6	0,001
0.004	7	0,001
0.004	8	0,001
0.005	9	0,001
0.006	10	0,001
0.006	11	0,001
0.006	12	0,001
0.008	13	0,002
0.009	14	0,002
0.011	15	0,002
0.011	16	0,002
0.012	17	0,002
0.013	18	0,002
0.013	19	0,002
0.015	20	0,002
0.015	21	0,003
0.016	22	0,003
0.016	23	0,003
0.017	24	0,003
0.017	25	0,003
0.017	26	0,003
0.018	27	0,003
0.018	28	0,003
0.019	29	0,003
0.02	30	0,004
0.02	31	0,004
0.022	32	0,004
0.022	33	0,004
0.023	34	0,004
0.025	35	0,004
0.028	36	0,004
0.028	37	0,004
0.028	38	0,005
0.029	39	0,005
0.035	40	0,005
0.035	41	0,005
0.035	42	0,005
0.038	43	0,005
0.04	44	0,005
0.041	45	0,005
0.041	46	0,005
0.041	47	0,006
0.043	48	0,006
0.046	49	0,006
0.046	50	0,006
0.046	51	0,006
0.049	52	0,006
0.051	53	0,006
0.055	54	0,006
0.059	55	0,007
0.062	56	0,007
0.062	57	0,007
0.064	58	0,007
0.067	59	0,007
0.068	60	0,007
0.068	61	0,007
0.072	62	0,007
0.072	63	0,008
0.072	64	0,008
0.074	65	0,008
0.077	66	0,008
0.078	67	0,008
0.079	68	0,008
0.081	69	0,008
0.081	70	0,008
0.081	71	0,008
0.084	72	0,009
0.084	73	0,009
0.084	74	0,009
0.084	75	0,009
0.088	76	0,009
0.091	77	0,009
0.096	78	0,009
0.097	79	0,009
0.1	80	0,010
0.1	81	0,010
0.108	82	0,010
0.108	83	0,010
0.108	84	0,010
0.113	85	0,010
0.113	86	0,010
0.12	87	0,010
0.12	88	0,010
0.123	89	0,011
0.124	90	0,011
0.125	91	0,011
0.126	92	0,011
0.128	93	0,011
0.132	94	0,011
0.135	95	0,011
0.137	96	0,011
0.14	97	0,012
0.141	98	0,012
0.143	99	0,012
0.146	100	0,012
0.154	101	0,012
0.158	102	0,012
0.163	103	0,012
0.164	104	0,012
0.17	105	0,013
0.171	106	0,013
0.171	107	0,013
0.175	108	0,013
0.18	109	0,013
0.181	110	0,013
0.185	111	0,013
0.187	112	0,013
0.189	113	0,013
0.189	114	0,014
0.191	115	0,014
0.192	116	0,014
0.194	117	0,014
0.195	118	0,014
0.199	119	0,014
0.204	120	0,014

p	*Rank*	*B-H*
0.204	121	0,014
0.209	122	0,015
0.209	123	0,015
0.212	124	0,015
0.213	125	0,015
0.214	126	0,015
0.221	127	0,015
0.225	128	0,015
0.227	129	0,015
0.228	130	0,015
0.229	131	0,016
0.232	132	0,016
0.232	133	0,016
0.235	134	0,016
0.237	135	0,016
0.241	136	0,016
0.242	137	0,016
0.245	138	0,016
0.246	139	0,017
0.247	140	0,017
0.252	141	0,017
0.255	142	0,017
0.256	143	0,017
0.26	144	0,017
0.261	145	0,017
0.262	146	0,017
0.275	147	0,018
0.275	148	0,018
0.278	149	0,018
0.279	150	0,018
0.282	151	0,018
0.286	152	0,018
0.293	153	0,018
0.293	154	0,018
0.293	155	0,018
0.296	156	0,019
0.3	157	0,019
0.301	158	0,019
0.302	159	0,019
0.302	160	0,019
0.309	161	0,019
0.313	162	0,019
0.314	163	0,019
0.315	164	0,020
0.317	165	0,020
0.318	166	0,020
0.319	167	0,020
0.325	168	0,020
0.331	169	0,020
0.332	170	0,020
0.334	171	0,020
0.334	172	0,020
0.334	173	0,021
0.343	174	0,021
0.346	175	0,021
0.348	176	0,021
0.353	177	0,021
0.356	178	0,021
0.356	179	0,021
0.363	180	0,021
0.365	181	0,022
0.366	182	0,022
0.367	183	0,022
0.368	184	0,022
0.371	185	0,022
0.372	186	0,022
0.38	187	0,022
0.381	188	0,022
0.381	189	0,023
0.382	190	0,023
0.382	191	0,023
0.384	192	0,023
0.388	193	0,023
0.39	194	0,023
0.39	195	0,023
0.392	196	0,023
0.393	197	0,023
0.397	198	0,024
0.397	199	0,024
0.397	200	0,024
0.398	201	0,024
0.401	202	0,024
0.404	203	0,024
0.408	204	0,024
0.41	205	0,024
0.417	206	0,025
0.422	207	0,025
0.426	208	0,025
0.426	209	0,025
0.428	210	0,025
0.429	211	0,025
0.431	212	0,025
0.433	213	0,025
0.435	214	0,025
0.439	215	0,026
0.44	216	0,026
0.445	217	0,026
0.445	218	0,026
0.447	219	0,026
0.448	220	0,026
0.451	221	0,026
0.459	222	0,026
0.459	223	0,027
0.46	224	0,027
0.462	225	0,027
0.462	226	0,027
0.464	227	0,027
0.471	228	0,027
0.472	229	0,027
0.476	230	0,027
0.483	231	0,028
0.485	232	0,028
0.486	233	0,028
0.486	234	0,028
0.489	235	0,028
0.499	236	0,028
0.5	237	0,028
0.5	238	0,028
0.501	239	0,028
0.503	240	0,029
0.505	241	0,029
0.507	242	0,029
0.51	243	0,029
0.51	244	0,029
0.511	245	0,029
0.514	246	0,029
0.514	247	0,029
0.514	248	0,030
0.515	249	0,030
0.519	250	0,030
0.521	251	0,030
0.523	252	0,030
0.524	253	0,030
0.524	254	0,030
0.526	255	0,030

p	*Rank*	*B-H*
0.529	256	0,030
0.531	257	0,031
0.535	258	0,031
0.536	259	0,031
0.537	260	0,031
0.539	261	0,031
0.547	262	0,031
0.547	263	0,031
0.555	264	0,031
0.563	265	0,032
0.564	266	0,032
0.576	267	0,032
0.58	268	0,032
0.583	269	0,032
0.584	270	0,032
0.592	271	0,032
0.595	272	0,032
0.598	273	0,033
0.6	274	0,033
0.605	275	0,033
0.613	276	0,033
0.614	277	0,033
0.614	278	0,033
0.615	279	0,033
0.62	280	0,033
0.621	281	0,033
0.622	282	0,034
0.623	283	0,034
0.625	284	0,034
0.627	285	0,034
0.628	286	0,034
0.628	287	0,034
0.629	288	0,034
0.632	289	0,034
0.633	290	0,035
0.634	291	0,035
0.635	292	0,035
0.649	293	0,035
0.653	294	0,035
0.654	295	0,035
0.655	296	0,035
0.659	297	0,035
0.66	298	0,035
0.661	299	0,036
0.661	300	0,036
0.666	301	0,036
0.666	302	0,036
0.667	303	0,036
0.668	304	0,036
0.673	305	0,036
0.674	306	0,036
0.676	307	0,037
0.676	308	0,037
0.677	309	0,037
0.678	310	0,037
0.678	311	0,037
0.679	312	0,037
0.68	313	0,037
0.682	314	0,037
0.683	315	0,038
0.691	316	0,038
0.692	317	0,038
0.7	318	0,038
0.704	319	0,038
0.708	320	0,038
0.709	321	0,038
0.71	322	0,038
0.716	323	0,038
0.722	324	0,039
0.728	325	0,039
0.728	326	0,039
0.731	327	0,039
0.732	328	0,039
0.733	329	0,039
0.736	330	0,039
0.741	331	0,039
0.742	332	0,040
0.747	333	0,040
0.751	334	0,040
0.754	335	0,040
0.756	336	0,040
0.76	337	0,040
0.76	338	0,040
0.761	339	0,040
0.761	340	0,040
0.769	341	0,041
0.769	342	0,041
0.771	343	0,041
0.771	344	0,041
0.776	345	0,041
0.778	346	0,041
0.782	347	0,041
0.783	348	0,041
0.787	349	0,042
0.792	350	0,042
0.792	351	0,042
0.793	352	0,042
0.804	353	0,042
0.811	354	0,042
0.818	355	0,042
0.823	356	0,042
0.823	357	0,043
0.826	358	0,043
0.834	359	0,043
0.835	360	0,043
0.837	361	0,043
0.841	362	0,043
0.844	363	0,043
0.847	364	0,043
0.851	365	0,043
0.856	366	0,044
0.858	367	0,044
0.858	368	0,044
0.861	369	0,044
0.873	370	0,044
0.874	371	0,044
0.875	372	0,044
0.877	373	0,044
0.88	374	0,045
0.884	375	0,045
0.885	376	0,045
0.885	377	0,045
0.886	378	0,045
0.886	379	0,045
0.889	380	0,045
0.891	381	0,045
0.894	382	0,045
0.894	383	0,046
0.895	384	0,046
0.895	385	0,046
0.897	386	0,046
0.898	387	0,046

p	*Rank*	*B-H*
0.9	388	0,046
0.906	389	0,046
0.906	390	0,046
0.907	391	0,047
0.908	392	0,047
0.908	393	0,047
0.911	394	0,047
0.913	395	0,047
0.915	396	0,047
0.916	397	0,047
0.918	398	0,047
0.924	399	0,048
0.924	400	0,048
0.93	401	0,048
0.935	402	0,048
0.938	403	0,048
0.942	404	0,048
0.945	405	0,048
0.947	406	0,048
0.958	407	0,048
0.959	408	0,049
0.96	409	0,049
0.964	410	0,049
0.966	411	0,049
0.967	412	0,049
0.969	413	0,049
0.973	414	0,049
0.975	415	0,049
0.986	416	0,050
0.988	417	0,050
0.991	418	0,050
0.992	419	0,050
0.999	420	0,050

Table A6: Benjamini-Hochberg correction on the correlations of the winds vs currents data. (*i/m*)**Q* = Benjamini-Hochberg critical value where *i* = Rank, *m* = total number of tests, and Q = false discovery rate of 0.05. The bold row shows the cut-off point of significance.

p	*Rank*	*B-H*
<0.001	1	0,001
<0.001	2	0,003
<0.001	3	0,004
<0.001	4	0,005
<0.001	5	0,006
<0.001	6	0,008
<0.001	7	0,009
<0.001	8	0,010
<0.001	9	0,011
<0.001	10	0,013
<0.001	11	0,014
<0.001	12	0,015
<0.001	13	0,016
<0.001	14	0,018
<0.001	15	0,019
<0.001	16	0,020
<0.001	17	0,021
<0.001	18	0,023
<0.001	19	0,024
<0.001	20	0,025
<0.001	21	0,026
<0.001	22	0,028
<0.001	23	0,029
<0.001	24	0,030
<0.001	25	0,031
0.002	26	0,033
0.002	27	0,034
0.010	28	0,035
0.018	29	0,036
0.021	30	0,038
0.023	31	0,039
0.034	32	0,040
0.038	33	0,041
0.085	34	0,043
0.089	35	0,044
0.093	36	0,045
0.172	37	0,046
0.183	38	0,048
0.285	39	0,049
0.795	40	0,050

Table A7: Benjamini-Hochberg correction on the correlations of all the taxa analysed. (*i/m*)**Q* = Benjamini-Hochberg critical value where *i* = Rank, *m* = total number of tests, and Q = false discovery rate of 0.05. The bold row shows the cut-off point of significance.

p	*Rank*	*B-H*
<0.001	1	0,000
<0.001	2	0,001
<0.001	3	0,001
<0.001	4	0,002
<0.001	5	0,002
<0.001	6	0,003
<0.001	7	0,003
<0.001	8	0,004
0.001	9	0,004
0.002	10	0,005
0.002	11	0,005
0.003	12	0,006
0.003	13	0,006
0.004	14	0,006
0.006	15	0,007
0.007	**16**	**0,007**
0.008	17	0,008
0.008	18	0,008
0.009	19	0,009
0.009	20	0,009
0.011	21	0,010
0.014	22	0,010
0.014	23	0,011
0.016	24	0,011
0.024	25	0,012
0.027	26	0,012
0.027	27	0,013
0.029	28	0,013
0.033	29	0,013
0.039	30	0,014
0.042	31	0,014
0.047	32	0,015
0.052	33	0,015
0.054	34	0,016
0.055	35	0,016
0.061	36	0,017
0.064	37	0,017
0.066	38	0,018
0.067	39	0,018
0.071	40	0,019
0.08	41	0,019
0.089	42	0,019
0.102	43	0,020
0.111	44	0,020
0.115	45	0,021
0.122	46	0,021
0.131	47	0,022
0.149	48	0,022
0.152	49	0,023
0.165	50	0,023
0.212	51	0,024
0.213	52	0,024
0.215	53	0,025
0.215	54	0,025
0.226	55	0,025
0.243	56	0,026
0.257	57	0,026
0.266	58	0,027
0.276	59	0,027
0.295	60	0,028
0.296	61	0,028
0.298	62	0,029
0.302	63	0,029
0.306	64	0,030
0.308	65	0,030
0.308	66	0,031
0.325	67	0,031
0.359	68	0,031
0.372	69	0,032
0.394	70	0,032
0.4	71	0,033
0.403	72	0,033
0.416	73	0,034
0.42	74	0,034
0.444	75	0,035
0.469	76	0,035
0.482	77	0,036
0.494	78	0,036
0.504	79	0,037
0.506	80	0,037
0.512	81	0,038
0.567	82	0,038
0.57	83	0,038
0.58	84	0,039
0.591	85	0,039
0.594	86	0,040
0.606	87	0,040
0.63	88	0,041
0.645	89	0,041
0.687	90	0,042
0.687	91	0,042
0.692	92	0,043
0.706	93	0,043
0.707	94	0,044
0.727	95	0,044
0.727	96	0,044
0.733	97	0,045
0.733	98	0,045
0.751	99	0,046
0.757	100	0,046
0.768	101	0,047
0.772	102	0,047
0.78	103	0,048
0.823	104	0,048
0.824	105	0,049
0.83	106	0,049
0.837	107	0,050
0.978	108	0,050

Chapter 5

Table A8: Benjamini-Hochberg correction on the permanovas examining the effects of temperature on oxygen consumption of mussel recruits. (*i/m*)**Q* = Benjamini-Hochberg critical value where *i* = Rank, *m* = total number of tests, and Q = false discovery rate of 0.05. The bold row shows the cut-off point of significance.

p	*Rank*	*B-H*
0.001	1	0.003
0.001	2	0.007
0.001	3	0.010
0.001	4	0.013
0.001	5	0.017
0.003	6	0.020
0.005	**7**	**0.023**
0.085	8	0.027
0.163	9	0.030
0.178	10	0.033
0.194	11	0.037
0.233	12	0.040
0.407	13	0.043
0.704	14	0.047
0.818	15	0.050